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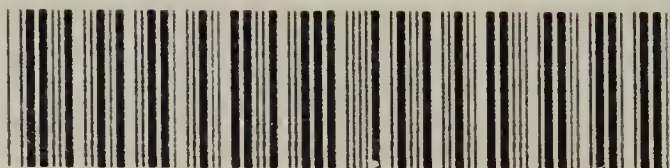
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# SCIENCE PROGRESS



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# Science Progress

*A QUARTERLY REVIEW*

OF

*CURRENT SCIENTIFIC INVESTIGATION*

CONDUCTED BY

SIR HENRY BURDETT, K.C.B.

EDITED BY

J. BRET LAND FARMER, M.A.

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# Science Progress.

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OCTOBER, 1896.

Vol. I.

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## SCIENTIFIC WEATHER FORECASTING.

THERE is hardly any kind of writing which so abounds with pitfalls as the history of scientific progress. Questions of priority arise in every few lines, and a writer who is worth his salt knows two things—(i.) that he had better not write at all unless he can improve greatly upon what has been written before, and (ii.) that the next man who attempts it ought to do better still.

Weather forecasting, after a fashion, has gone on for thousands of years, and some of the rules of the Hebrews, Greeks and Romans, preserved in the Bible and in the writings of Aristotle, Theophrastus and Aratus, may justly be called scientific, as they represent definite conclusions drawn from physical facts. The special object of the present article is historical, to show how Scientific Weather Forecasting became possible, rather than how it is at present being done in nearly every country in the world.

But, by those who have not previously considered the subject, the historical points will be more readily appreciated if a very brief and elementary sketch be given of the method now adopted.

Each country has a central office and a considerable number of small observatories—stations they are generally called—scattered widely apart over its territories, preferably on the sea-coast, but always at places whence there is electro-telegraphic communication with the central office. At each of these stations there is at least one good baro-



meter and thermometer—at the majority of them there are a full set of meteorological instruments and some in duplicate. The observer has to read the instruments at specified hours, and to telegraph the results to the central office.

At the central office, the observations from each station are (after the application of any necessary corrections) marked upon a map; the barometer and thermometer in figures, the wind by an arrow flying with the wind, and with barbs proportional to the strength of the wind. These entries are made over the spot upon the map which represents the station whence those data came. When all the reports have arrived, lines are drawn joining places at which the barometric pressure is the same (isobars), and through those of which the temperature is the same (isotherms). A distinct relation is immediately evident between these isobars and the arrows representing the direction and force of the wind. Roughly, the arrows are parallel with the isobars, and they are more barbed—*i.e.*, the wind is stronger—the closer the isobars are together.

Generally these isobars are curved, and enclose an area either of low or of high barometric pressure. In the former case there is said to be a cyclone; in the latter, an anti-cyclone. If the central barometric pressure be very low and the isobars close together, a violent storm is in progress; if the central pressure be high and the isobars wide apart there is a calm, and, in winter, generally a fog.

These cyclonic and anti-cyclonic systems move about, chiefly in easterly directions, but they do not move with the speed of the telegraph, and, consequently, if it were possible to know the direction, and the rate, of their movement, it would be possible to state where the centre would be at a given time, and from that knowledge to state what weather would prevail at any given spot, because the weather characteristics of each quadrant of a cyclone are known. The difficulty for the forecaster is, to tell in what direction and at what speed the system will move, and whether it will increase or decrease in intensity. This is not easy even in the United States, where, generally, the systems can be watched from their birth in the Rocky Mountains until they pass away on to the Atlantic; but for the British Isles and



for France, which have no stations to the West of them, it is extremely difficult. There are, moreover, "V shaped depressions," "secondaries," and other varieties of distribution of pressure to be detected and taken into account, so that on the whole a British forecaster probably requires boldness as much as he needs knowledge.

From the above very brief sketch of the principles of Scientific Weather Forecasting, it will be seen that the essentials are—(i.) Knowledge of the general principles of atmospheric circulation ; (ii.) the use of weather maps ; (iii.) the use of the electric telegraph.

The fact that storm systems travel towards the east was noticed at a very early date. Mr. R. H. Scott, F.R.S. (1) says :—

"The earliest notice of it which we can discover is an entry on the map of Virginia, published in 1747 by Lewis Evans, to the effect that 'all our great storms begin to leeward'. Franklin, in 1760, followed in the same strain, but it appears that his attention had been caught at an earlier period, in 1743, by the fact of his being prevented at Philadelphia, by the clouds brought by a hurricane, from observing a lunar eclipse, while the eclipse was seen at Boston, which lies farther to the north-eastward, before the storm came on."

The first proposals towards the existing arrangements seem to have been those of Lavoisier (2) about 1780, but his suggestion included little knowledge of the laws of atmospheric circulation, no weather map, and no electric telegraph. He knew that a falling barometer generally indicated wet weather, and a rising one fine weather, and suggested that predictions based upon the motion of a single barometer might be sent daily for publication in a newspaper. Romme in 1793 (3) carried the proposal farther, and suggested the use of Chappe's Aerial Telegraph to "enable physicists to foresee the arrival of storms, and to give notice of them to the ports and to farmers".

It is incapable of proof, but not improbable, that the foregoing suggestions, and the investigation next to be mentioned, were indirectly connected with the great work carried out about that date by the Meteorological Society

of the Palatinate in the publication of the Mannheim Ephemerides. In 1801 appeared Colonel Capper's work (4) upon the results of his observations upon the coast of Coromandel, in which he lays down the circular character of the motion of the winds.

In 1820 Professor H. W. Brandes of Breslau published an important work (5) in which he discussed, with great labour and skill, daily records for the year 1783 from thirty stations, twenty-eight in Europe and two in America. It is curious to notice how closely he approached modern methods ; for instance, a storm and barometric depression passed from the British Isles to Berlin from about the 6th to the 9th of February, and although in his book he does not give a chart, it is almost certain that he must have drawn one, with something identical in appearance with our modern isobars. The modern practice of reducing barometer readings to their equivalent sea level pressures had not been thought of, but instead, Professor Brandes adopted the plan (much later employed by Buijs Ballot) of expressing the readings as departures from the average. To show how thoroughly he had seized the idea of isobars a few words must be quoted :—

“ Am tiefsten, nämlich 14 Linien unter der Mittelhöhe stand das Barometer in Lyndon in Rutlandshire. Die gegend, wo es  $13\frac{1}{2}$  Linien unter der Mittelhöhe stand, lässt sich durch eine Linie bezeichnen, die etwas westlich von Franeker, genau über Amsterdam und dann vermuthlich das südliche England geht. Die Linie wo es 13 Linien zu tief stand, geht noch oberhalb Mittelburg, über den Canal, nach dem französischen Hafen St. Malo.”

Professor Brandes similarly traces the lines joining the gradually less and less depressions until he reaches a depression of only three lines at Bologna and Rome. In another place he regrets that he had not sufficient information similarly to study the direction and strength of the wind, he says that where the barometer was lowest the wind was strongest, that the depression occurred earlier on the Atlantic coast than in the East, and he anticipated the modern idea of barometric gradient by comparing the depression at different places and dividing it by their dis-



tance and then trying to get out the resultant velocity of the wind.

All this be it remembered was published in 1820, and therefore was probably done some years before. In 1830 Redfield in the United States announced that (i.) storms were approximately circular (ii.) travelled north-eastwards (iii.) increased in strength towards the centre ; but (iv.) became calm at the centre, and he illustrated this by a diagram (6).

From about 1830, Col. (afterwards Sir Wm.) Reid was at Bermuda, and in his *Law of Storms* (7) he says :—

“ A very interesting mode of testing the Law of Storms is that of considering the probable line of progression of gales in their passage. It was thus that I (Col. Reid) was in the habit of studying the winds at Bermuda for nearly eight years, and that Mr. Redfield has studied them at New York for a much longer period. In September, 1839, Mr. Redfield wrote to me from New York, when he first heard of the gale of that year, that he thought it must have passed over Bermuda ; and this was before he could have heard from these islands. A reference to the plate will show how correct his judgment was, for the centre touched the westernmost part of the islands.”

From 1830 onwards, the construction of weather maps was general with leading meteorologists, such as Espy, Piddington, Redfield and Reid ; but these, it must be remembered, all referred to dates far anterior to their construction. The electric telegraph was not invented until 1837, and it was not until a much later date that its use was sufficiently extensive and cheap to allow meteorologists to avail themselves of it.

The first proposal for the use of the telegraph, and of synchronous observations for weather forecasting, which we can trace, was by Carl Kreil in 1842, when he was assistant at Prague Observatory (8). It is much too long for reproduction, but points out the necessity for having distant stations ; that the optical telegraph was scarcely sufficiently rapid and could not be used at night, but that the recently discovered electro-magnetic telegraph, as soon as it had been brought into general use, would precisely meet the case, and he illustrates the method by the passage of the



storm of 17th and 18th July, 1841, from South Italy to Prague in about thirty hours.

Closely connected with weather forecasting are arrangements on the coast for indicating to passing vessels the height of the barometer, or the character of weather likely to prevail. The earliest note of this kind which we have seen was in a fragment of the *Carnarvon Herald* (9) for 1841 or 1842, in which an anonymous writer proposed the erection of an indicator with a circular dial, 3 ft. in diameter, divided somewhat like a wheel barometer, and with a bar (corresponding in position to the hand of a wheel barometer, but) projecting 1 ft. 6 in. beyond the dial.

This was a proposal only ; five years later Col. Reid had another arrangement in actual work. We give his account verbatim (10) :—

“In 1847 I had the satisfaction of establishing signals at Barbados to give warning of approaching hurricanes, and of publishing at the same time suggestions as to the direction in which ships should be steered when quitting Carlisle Bay at the setting in of a hurricane”.

Then follows a reprint of the official notice, whence we can quote only the first four paragraphs :—

“A barometer is kept and registered at the principal police station at Bridgetown, Barbados, and notice will be given to the captain of the port when it falls. On the captain of the port rests the responsibility of causing signals to be hoisted that the barometer indicates bad weather.

“One ball at the masthead of the signal-posts is to signify that the barometer is falling, and should be carefully watched.

“If the barometer continues to fall and the weather appears threatening, a second ball will be hoisted at the masthead.

“As the indications of the weather become alarming, these two balls will be gradually lowered until they are only half-mast high.”

Until within the last thirty or forty years, meteorologists in one country knew far too little of what was being done in other countries. For instance, it is almost certain that neither Fitz Roy, Glaisher, nor Le Verrier ever read the statement by Kreil, which we have mentioned earlier in this

article, and which had been printed years before they took action in the matter. This lack of inter-communication, and difficulties arising from the use of different languages, should not be forgotten, because it makes many discoveries really independent which, looked at chronologically, appear successive.

The first actual use of the electric telegraph for the transmission of information respecting the weather seems to have been in America, as Professor Henry, the Secretary of the Smithsonian Institution, in 1849, personally requested the telegraph companies to direct their operators to replace in their regular morning despatches the signal "OK" (by which they were accustomed to announce that their lines were in order) by such words as "fair," "cloudy," etc., thus giving without additional trouble, and as concisely as possible, a summary of the condition of the weather at the different stations, and which should be communicated to him (11).

This, it will be noticed, was weather *only*, and no map was made representing the information. Wind direction was, we believe, not sent to Washington till 1858, and at that date the information was marked on a large map by moveable discs.

Synchronously with Professor Henry's action in the United States, or possibly slightly before it, Mr. Glaisher, F.R.S., was organising, by the joint action of the Electric Telegraph Company, the Railway Clearing House, and the proprietors of the *Daily News*, a really scientific system in this country. Furnished with a pass over nearly every railway in the country, he went to all the terminal stations of the Electric Telegraph Company, and to many of the intermediate ones, determined a meridian line for each and instructed the clerks as to observing the direction of the wind, and reporting the state of the weather.

The first publication was in the *Daily News* of 14th June, 1849, when a table was inserted giving the direction and strength of the wind and the state of the weather at thirteen stations, and the following footnote. "As explained elsewhere<sup>1</sup> the very extensive arrangements for making this table complete have not yet been concluded. In a short time we shall

<sup>1</sup> But no such explanation can be found.



present daily returns from thirty-nine stations extending from Plymouth to Glasgow and from Yarmouth to Holyhead."

In 1851 came the Great Exhibition, and the exhibit of the Electric Telegraph Company consisted of a large map on which were daily indicated the direction of the wind and the state of the weather at about thirty of their stations, and also of daily reproductions by lithography which were sold at a penny a copy. These were the first maps of current weather ever issued, and notwithstanding that there are no isobars and the barometer readings were not reduced to sea level (although Mr. Glaisher had, in the tables supplied to the Registrar General, adopted this excellent plan as early as 1849), the clean sharpness of the printing makes these maps extremely interesting. Unfortunately their publication ceased when, or slightly before, the Exhibition closed. The issue extended from 8th August to 11th October, 1851, with the exception of Sundays. A few perfect copies of the entire set have been preserved.

Placing ourselves in imagination in the latter part of 1851, we find nearly every part of the modern system suggested, or in operation; the circular theory of storms, their easterly progression, their calm centre, isobars and the dependence of wind force on their proximity (now called the barometric gradient), the construction of weather maps from synchronous observations on the same day, the prediction of future based upon the knowledge of existing weather, and the communication to ships of information gained upon land.

Consequently though we should be the last to depreciate the work of Buijs Ballot, Le Verrier, Fitz Roy and their successors, and though doubtless much of their work was original with them, still there is no need now to dwell much upon it.

We believe that the first Government to take action in the matter of collecting data by telegraph was that of Holland, on the recommendation of Buijs Ballot, in or about 1855, and that they very shortly followed this by sending announcements of coming storms.

France, at the suggestion of Le Verrier, organised an analogous system in the same year.

England came third, beginning under Admiral Fitz



Roy, as the result of a suggestion by Le Verrier in 1860. It will probably be of interest to reproduce from the *Times* the first daily weather report issued by the Meteorological Office, that for 5th September, 1860.

THE WEATHER.								
METEOROLOGICAL REPORTS.								
Sept. 5, 9 A.M.			B.	E.	M.	D.	F.	C.    ⚡
Greenock	.....	.....	30·21	59	58	W.S.W.	2	0    b.
Berwick	.....	.....		59	58	W.	2	—    —
Galway	.....	.....	30·34	59	58	N.W.	2	8    b.c.
Hull	.....	.....	30·15	59	57	W.	2	2    b.
Yarmouth	.....	.....	30·15	58	57	N.W.	3	0    b.
London	.....	.....	30·26	60	55	W.	3	3    b.c.
Dunkirk	.....	.....	30·32	58	52	W.	0	0    b.
Portsmouth	.....	.....	30·30	54	54	N.	1	4    b.c.
Plymouth	.....	.....	30·20	60	59	W.	1	3    b.c.
Penzance	.....	.....		64	62	N.	2	2    b.o.
Cherbourg	.....	.....	30·32	60	53	—	—	2    b.c.
Havre	.....	.....		54	—	W.	0	1    b.m.
Jersey	.....	.....	30·30	61	57	N.	2	5    b.c.
Brest	.....	.....	30·09	59	50	N.W.	—	3    b.c.
Explanation.								
B. Barometer, corrected and reduced to freezing, at mean sea level. E. Exposed thermometer. M. Moistened bulb. D. Direction (true) of wind. F. Force (0 to 12). C. Cloud (0 to 10). ⚡ Initial letter of appearance in sky (by Beaufort method).								
M. O.								
(BY ELECTRIC AND INTERNATIONAL TELEGRAPH.)								
WIND AND WEATHER REPORT AT 8 O'CLOCK YESTERDAY								
EVENING.								
Inverness, S.W. ; fine.			Manchester, N.W. ; dull.					
Aberdeen, N. ; dull.			Southampton, calm ; cloudy.					
Dundee, calm ; fine.			Weymouth, calm ; cloudy.					
Edinburgh, W. ; foggy.			Plymouth, N.W. ; fine.					
Berwick, N. ; foggy.			Bristol, E. ; fine.					
Newcastle-on-Tyne, W. ; fine.			Cardiff, W.N.W. ; fine.					
Hartlepool, S.E. ; fine.			Holyhead, N.W., calm ; cloudy.					
York, N. ; fine.			Liverpool, W.N.W. ; cloudy.					
Hull, E. ; fine.			Glasgow, N. ; fine.					
Derby, N. ; dull.			Jersey, N.W. ; very fine.					
Peterborough, N.E. ; dull.			Colchester, W. ; fine.					
Yarmouth, N.N.E. ; dull.			Leeds, W. ; fine.					
Harwich, N. ; fine.								

It will be noticed that there are in the above two reports—Admiral Fitz Roy's for 9 A.M., 5th September, 1860, and the Telegraph Company's report for 8 P.M. on the same day.

Within six months of the receipt of his first telegrams Admiral Fitz Roy had gained sufficient confidence in his organisation to issue a warning of a coming storm (February, 1861), and within a year he began to issue (August, 1861) forecasts of coming weather. This rapid progress drew public attention to the subject and, but for the want of funds, this country would (as it so often has done) have gone ahead of its own Government, and again by private enterprise been first of any country in the world to produce a daily telegraphic weather map. We should, if possible, have given the names of those who promoted the company which desired to do this, but we have only the prospectus and the map for 5th August, 1861, and it bears no name. The scheme was extremely ingenious, and the map could have been issued in London within three hours of the observations being taken in any part of the British Isles. The map was about twenty inches by fifteen inches, and contained records from sixty-two stations well distributed from Penzance to Nairn, and from Galway to Yarmouth. The map was to be printed from an ordinary press, the outline names of stations, etc., being on a large block, with an octagonal hole for each station, through which hole the appropriate symbol was passed, and when all had been put in position, the map was ready for printing. The symbols were very simple, three varieties of outline showed whether the barometer was rising, stationary or falling, the letter C and four varieties of arrows showed the force of the wind, while its direction was shown by that of the arrows, and five systems of ground (dots, rings, etc.), showed whether the sky was clear, partly cloudy, overcast, showery, or continuously rainy. Some one must have lost heavily, for all the necessary instruments were made by Negretti and Zambra, verified by Mr. Glaisher, and conveyed to their destinations, the map and symbols were prepared and engraved, but the funds for the issue of the *Daily Weather Map and Journal* were not obtained, Admiral Fitz Roy would not (or was not allowed to) help, and so the scheme fell through, and England which had been the first to produce one was left without a daily weather map for

twenty-one years, until at last in 1872 the English Meteorological Office consented to issue one.

But in France Le Verrier was aware of the importance of such an issue from the first, and France published its first Daily Map of the Weather as early as 16th September, 1863, and the United States followed in January 1871, so that as regards official publication England was third instead of being first.

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## THE NATURAL HISTORY OF IGNEOUS ROCKS: I. THEIR GEOGRAPHICAL AND CHRONOLOGICAL DISTRIBUTION.

INTENDING in this and succeeding papers to glance at some of the modern aspects of petrology in relation to igneous rocks, we shall begin by considering briefly the distribution of the rocks in time and space. In studying the geology of particular regions this subject has often been passed over, even by eminent authorities, with but slight notice. Indeed it must be admitted that in general igneous rocks are accorded a rather unceremonious treatment. Too often they are relegated to an appendix in a memoir or monograph, as if they were without significance in the geological history of the district where they occur. They are indeed indicated as regards their situation on geological maps, but only with a colour denoting more or less correctly their petrographical nature. Often we see, on otherwise carefully drawn up maps, a common legend of "volcanic rocks," applied alike to Tertiary basalts and Palæozoic rhyolites and andesites. It is curious to note that while stratigraphy has, so far as the sedimentary rocks are concerned, replaced the old-fashioned "geognostic" maps by those expressing in the first place chronological sequence, no such change has been made in the mode of representing the igneous rocks. It is not a little instructive, as will be found by any one who will test it, to construct maps on which the igneous rocks, whether interbedded or intruded, are marked in the colours adopted for the stratified formations of like age. The distinction between intruded and interbedded, and, if desired, between acid and basic rocks, etc., can be rendered by different tints and hachures.

The subject is one of considerable importance to the physical geographer as well as to the geologist, if indeed these are to be regarded as two distinct individuals. Although volcanoes have been studied from a very early time, and in some respects with great thoroughness, some of the

most fundamental points concerning them are still involved in doubt. Their geographical and local distribution is one such question. It is a familiar fact that the arrangement of volcanic vents at the present day is in general a linear one, giving place in some regions to a disposition in groups; further, that the lines often correspond very evidently with coast-lines, while the groups are often island-groups. On these and other data some have based theories of the situation of the vents on lines of fracture in the earth's crust, while others have speculated upon an accession of sea-water as the proximate cause of volcanic eruptions; but such hypotheses rest at present upon a very slender basis of ascertained fact. Other questions arise when we examine the products ejected by modern volcanoes. On the one hand, we find throughout a vast tract, such as the Andes, all the volcanic rocks closely related in characters and departing but little from a central type; on the other hand, a small group, such as that of the Æolian Isles, may afford varieties of lava of widely diverse and highly special characters. To such problems a study of modern volcanoes alone can scarcely hope to bring a satisfactory solution. It is necessary to inquire whether some empirical laws which seem to hold good are not rather to be regarded as parts of larger principles, and to seek for an explanation of present anomalies by viewing them as survivals of a pre-existing state of things.

In such a course, as in not a few modern geological inquiries, we are reversing the maxim of the school of Hutton and Lyell. Instead of applying a knowledge of the processes now going on around us to elucidate the record of past ages, we are making use of the history of the past to explain the phenomena of the present. Geology is thus repaying some of the debt which she owes to Physical Geography.

The frequent close connection of plutonic and intrusive rocks with surface vulcanicity is now scarcely called in question, though, in the nature of the case, instances must be few in which such connection can be directly demonstrated. Special stress was laid on this point by Judd in



his study of the Tertiary igneous rocks of the Inner Hebrides, and similar conclusions have been arrived at by Lotti in Elba and by various other geologists in the Andes and elsewhere. Of special importance in this connection are the researches of Hague and Iddings on the rocks of the Comstock Lode in Nevada. The extensive mining operations at that place enabled them to make a comparative study of the rocks through a very considerable vertical range, and they conclusively established the gradual transition in characters from andesitic rocks consolidated under practically superficial conditions to the plutonic equivalents of those rocks formed at greater depths and in the heart of the mass. Of interest, too, is the close correspondence, shown by Iddings (1) in the Yellowstone Park district, between the intrusive porphyrites and diorites of Electric Peak and the breccias and lavas of Sepulchre Mountain. Speaking generally, the geological evidence warrants us in affirming that igneous intrusions have occurred in districts of volcanic outbursts, and are so related in point of time to the latter as to indicate an essential connection between the two phenomena.

The growth of opinion concerning the petrology of igneous rocks has been, in recent years, mainly around two central ideas, *viz.*, the close relation subsisting between igneous activity and movements of the earth's crust, and the production under proper conditions of various rock-types from one original rock-magma. Neither of these ideas is strictly a new one. The former was insisted upon long ago by von Buch and others; but while those writers regarded volcanic outbursts as the causes of disturbances of the strata, modern geologists take rather the converse view. Again, the conception of differentiation in molten rock-magmas is at least as old as Durocher's famous theory; but only recently has the idea been developed with any attempt at completeness, and the practical application of it to a particular group of associated rocks had scarcely been ventured upon before Brögger's studies in the Christiania basin.

It is with the former of the two ideas just mentioned that we are here concerned. The work of Suess, Lossen,



Bertrand and many others has now given us a sufficient general idea of the nature, situations and epochs of the most important crust-movements during the times contemplated by the stratigraphical geologist, and it is possible to discuss to some extent the relation to these movements of the known groups of igneous rocks, both intrusive and extrusive. This has been done summarily for the European area by Bertrand in a memoir, published in 1888, which may be taken as a model for this kind of investigation (2). In a more restricted region, the geological history of which is sufficiently well known, the comparison may be developed in greater detail. For an application to our own country the data are furnished by Sir A. Geikie's account of volcanic action within the British area, contained in his Presidential Addresses to the Geological Society in 1891-92, and supplemented, as regards the Tertiary igneous rocks, by his memoir of 1888 (*Trans. Roy. Soc. Edin.*), and by the various papers of Judd.

Bertrand distinguishes in Europe four great systems of folding and disturbance of the stratified rocks; the earliest, the so-called Huronian, being here added to the Caledonian, Hercynian, and Alpine systems already recognised. The regions affected by these disturbances form broad zones, limited on the map by sweeping curves; and the several zones, while partially overlapping one another, successively advance further towards the equator. It seems probable that the first, and perhaps also the last, of these four systems must eventually be further divided, but Bertrand's statement of the broad facts affords meanwhile a basis for important generalisations. To the Huronian system belong crust-movements of pre-Palæozoic and early Palæozoic age, the first effects of which are seen in the north-western Highlands of Scotland and along the Norwegian coast, though the region ultimately involved had a considerably wider extent. The Caledonian (Upper Palæozoic) disturbances affected the greater part of what are now the British Isles as well as a belt extending north-eastward through Scandinavia. The main zone of Hercynian folding, marking the close of Palæozoic time, extends eastward

from the South of England and Brittany through Central Europe to Saxony and Silesia. To the latest (Tertiary) epoch of disturbance belongs the great Alpine system of mountain-chains, with its extensions into Asia and Northern Africa. The author makes it clear that each of these great systems of crust-movement has its own suite of volcanic, intrusive, and plutonic rocks, developed within the limits of the disturbed region, and in a general sense contemporaneous with the folding.

That this contemporaneity of igneous activity with disturbance of the solid earth-crust is to be understood in a general sense will be easily apparent. It is certain that movements of the kind considered proceed with extreme slowness, being prolonged, interrupted, and resumed during long periods of time ; and many observations go to prove that they are not simultaneously felt throughout their extent, but are gradually propagated in wave-like fashion through the crust of the earth. There is no difficulty in believing that the disturbances initiated in Eocene and Miocene times have in some regions not yet wholly subsided. Again the geological records of superficial volcanic action prove it in many districts to have been of long duration, with intervals of quiescence interrupted by renewed activity, and finally gradual extinction ; while there is good reason for supposing that the intrusion and complete consolidation of, say, a large body of granite implies a lapse of time not always to be included within the limits of one geological period. Regarding then the four, or more, distinct times of folding, not as decisive epochs, but rather as prolonged ages, having, however, a more or less defined era of maximum energy, and allowing a similar latitude as regards the associated manifestations of igneous activity, we may expect to find that in some cases the eruptions connected with one system of crust-movements overlap in time those belonging to another system, and that perhaps in districts not very widely separated. In such cases the true relations may appear only on a comprehensive view, embracing, for instance, the whole of the European area. Thus in the Midland Valley of Scotland igneous activity connected



with the Caledonian crust-movements was continued through a large part of the Carboniferous period and even in some districts into the Permian, while the Carboniferous and Permian igneous rocks occurring in many districts from the Loire Valley eastward to Saxony are clearly related to the Hercynian folding. It may be noted that, having regard to the petrographical characters of the rocks in question, the Scottish lavas and tuffs are mainly of basaltic nature, while acid types generally prevail among the volcanic rocks of the same general age within the Hercynian zone; although perhaps much weight should not be allowed to such considerations. The granites of Cornwall and Devon, it may be remarked, are to be grouped not with British occurrences farther north, but with those of Brittany, as members of the Hercynian series.

A point of equal importance is the frequent overlapping in space of the several zones of disturbance, or the tendency of a district already affected by a earlier set of movements to become involved in the operations of a later set. With this we may correlate the fact, emphasised by Geikie, that particular districts in the British Isles have been the theatre of a recrudescence of volcanic activity at several distinct and sometimes widely separated epochs. Numerous examples illustrating these two related principles might be cited in Scotland and Wales, and equally striking instances appear in other countries. Thus it is known that parts of the Alpine chains coincide with older lines of folding of Hercynian and perhaps greater age, and Bertrand has pointed out in the Tirolese area a belt of Permian and Triassic eruptive rocks branching off from the main Hercynian zone to follow exactly a line laid down as that of the "pre-Permian Alps" of that district. He has even maintained with much plausibility a tendency for anticlinal and synclinal axes of the newer folding to be not only parallel to, but actually superposed upon, like axes of the older folding. This hypothesis has attracted considerable attention owing to its important practical consequences. For instance, the search for coal in our south-eastern countries will be very materially forwarded if the folds of



the Mesozoic strata can be taken as an accurate guide to those of the older rocks which they conceal.

The close connection between crust-movements and igneous eruptions is exemplified not only by the constant association of igneous rocks with disturbed strata, but equally by the absence of such rocks from undisturbed districts. As instances of this we might point to very extensive tracts in Russia, the Mississippi basin, and other countries ; the significance of the fact being in some cases heightened by contrast with neighbouring districts, where the same strata, involved in a disturbed zone, are found to contain intercalated volcanic formations or to be traversed by dykes or other intrusions.

We are brought then to regard igneous rocks in general as in no wise meaningless interpolations in the stratigraphical sequence, but rather as closely bound up with the geological history of the districts in which they occur, and often in intimate relation with folds, faults, unconformities, and other geological accidents. Broadly viewed, they occur within large but defined regions of the globe co-extensive with the areas of operation of the crust-movements of which those same accidents are witnesses. Further, we are often able to divide one of these great regions into provinces of smaller, but still in some cases very extensive, dimensions ; these provinces being also defined with reference to the folding of the region, while their individuality is often marked by peculiarities, petrographical or otherwise, in which they differ from one another. The eruptions in one such province are not necessarily contemporaneous in a strict sense with those in another, and we shall see that different stages of development may co-exist in neighbouring provinces of one region. In one province, at least in the later stages of its history, we may recognise districts presenting distinctive features of their own and including perhaps one or more volcanic centres.

To illustrate what we have styled provinces of eruptive rocks we may take those belonging to the Alpine system in Europe. Within the zone of Alpine folding itself are four well-defined provinces ; the Tyrrhenian, extending from the

western portion of Italy westward, so as to include part of the African coast and the Cabo de Gata district in Spain; Hungary and Transylvania; Servia and Rhodope; and the Ægean, continuous towards the east with part of Asia Minor. Each of these areas is embraced by mountain-chains belonging to the Alpine system, and they occupy indeed the spaces left between the several branches where least compressed. Another group of provinces, in some cases less sharply defined, occurs just outside the northern border of the main belt of folding. To this belong Auvergne and Cantal; the Eifel and the Siebengebirge; Hesse, the Vogelsgebirge, and the Rhön; the Saxon Mittelgebirge, and Bohemia. Within the areas thus defined are districts containing volcanoes which have not long been extinct, while in the former group of provinces, *viz.*, in the lobes of the Mediterranean embraced by mountain-chains of the Alpine system, vulcanicity is still active at several centres.

It will be observed that the foregoing summary of the distribution of Tertiary and post-Tertiary igneous activity in this quarter of the globe is incomplete, in that it makes no mention of the British Islands. Antrim and the Inner Hebrides, with their Eocene igneous rocks, form part of a great province extending northwards into the Arctic regions, within which vulcanicity has been operative in Tertiary times, and in some districts has not yet died out. Further, this Brito-Icelandic province is itself only part of a region which also includes the Azores, Canaries, Cape Verd Islands, Ascension, St. Helena, and Tristan d'Acunha, with parts of the Portuguese and African coasts, thus stretching along the whole Atlantic border of the Old World. Unlike the others already noticed this region has a general meridional trend. Bertrand sees in this extra-Alpine region of Tertiary igneous rocks the illustration of a new principle, the operation of which is not to be seen, or at least is not clearly marked, in the earlier geological periods. The igneous rocks are still related to crust-movements, but in this case to those greater movements of which oceanic depressions and continental elevations are the results. We have indeed scattered relics



of a belt girdling the Atlantic, analogous to the much better defined "Circle of Fire" which surrounds the Pacific Ocean. Judd, following Nordenskjöld, long ago suggested that the volcanic rocks seen at so many points from Jan Mayen to Tristan d'Acunha may be regarded as portions of a ridge, now for the most part submerged, bordering the eastern continents as the volcanic belt of the Rocky Mountains, Cordilleras, and Andes does the western.

Taking now as an established principle the intimate relation between igneous rocks and crust-movements, whether of the mountain-building or of the continent-building order, we pass on to another branch of our subject, *viz.*, the idea of historical sequence in the various phenomena of igneous action. This may be viewed either from the physical or from the petrological aspect. The conception of a "life-history" of a volcano, divided into successive stages of development and decline, is not a new one, and it is capable of extension to districts, provinces, and regions of igneous rocks. The question whether such traces of a connected history are to be detected in the geological record as a whole is a more dubious one, and need not detain us at present. Those who see in this record evidences of a general decline in the energy of vulcanicity from Archæan times to the present day have perhaps been influenced to some extent by *a priori* reasoning on the physics of a gradually cooling globe.

The earlier stages in the igneous history of a disturbed region seem to have been marked usually by the intrusion of considerable bodies of molten magmas, often by violent superficial outbursts of a paroxysmal character, and generally by the approximately simultaneous extrusion of great quantities of lava at various centres over very extensive areas. The closing event as regards intrusive rocks has been the injection of fissures by dykes, which are often seen to traverse the earlier plutonic and large intrusive masses; while surface outbursts have been restricted in their later stages to diminishing and often isolated districts. The modern volcanoes of the Mediterranean area and of



Iceland, etc., regarded as survivals of the Tertiary volcanic era, are instances of this localisation; the Triassic eruptions of the southern Tirol stand in a similar relation to the Hercynian series, and the eruptions of Silurian age in Ireland and the Menez-Hom district of Brittany to a still older series. Sporadic volcanic centres, such as those of the puy<sup>s</sup> of Auvergne, and multitudes of small vents, like those whose craters are still preserved in the Eifel, are characteristic of a late phase in volcanic evolution. In the Carboniferous volcanic province of Scotland Geikie has expressly distinguished a period of "puy" eruptions following that of the more important and widely-spread "plateau" out-pourings. Moreover, he has identified in Fifeshire and East Lothian the sites of many of the old vents, now marked sometimes by masses of coarse agglomerate and breccia, sometimes by a plug of rock consolidated in the throat of the old volcano.

Von Richthofen has reminded us that we are not warranted in assuming the familiar apparatus of crater and cone to be a necessary and invariable concomitant of surface volcanic action, and it may be inquired whether this phase is related to a distinct stage in the evolution of a volcanic region. It is, of course, to be borne in mind that if volcanoes of what we commonly regard as the characteristic type have been formed in the earlier stages of activity of a given period, they may often have been obliterated subsequently or concealed beneath later accumulations, and indeed the destruction of old volcanoes by a revival of explosive action is a fact of which we have direct evidence. Reviewing, however, the rather scanty information at our disposal we are inclined to regard it as more than a chance coincidence that, where the actual structure of true volcanoes has been recognised among the older formations, it is always in connection with the later maturity and gradual waning of igneous activity. The case of Monzoni, described by numerous writers, is an example, and the same rule holds as regards the Carboniferous and Permian volcanoes of Scotland, and, still earlier, in the Lower Palæozoic volcanic districts of this country. In

Anglesey and in Wicklow Sir A. Geikie has identified numerous ancient vents, apparently of late Ordovician age, filled for the most part with masses of agglomerate. In Carnarvonshire erosion has exposed the relations at a deeper level, and the sites of the old volcanoes are now marked by intrusive bosses and plugs. Here and in similar cases the scarcity of true dykes seems to be a characteristic feature.

The last-named district is sufficient in itself to illustrate many features which seem to be characteristic of an evolution of an area of igneous activity, and, in particular, it exhibits with exceptional clearness the manner in which the several stages are bound up with the local crust-movements which brought the Ordovician period to a close. The linear disposition of the old orifices of eruption is well displayed on a geological map of the district. The line runs south-westward from near Penmaenmawr far down into the Lley peninsula, parallel to the axes of folding, and occupying precisely the position it should have if the eruptions were a consequence of the increasing thrust from the south-east (3). It will, of course, be observed that from our present point of view the frequent linear arrangement of volcanic vents, to which we adverted at the outset, connects itself directly with the distribution of stresses in the earth's crust, visibly expressed in axes of folding, etc. Whether or not the vents are situated upon actual lines of fissure is not an essential question, and the coincidence of many lines of volcanoes with coast-lines is equally a secondary feature.

The part played by so-called "massive" or "fissure" eruptions in the volcanic history of a region is scarcely to be estimated without more precise knowledge of their nature and characteristics than we at present possess. Some great out-pourings of lava which have been regarded in this light, such as the basalts of the Snake River plains, are certainly very late occurrences. If the numerous dykes which cut the Archæan of the north-west Highlands of Scotland have been the channels of fissure-eruptions, these would seem to have been among the latest manifestations of pre-Torridon igneous activity; though, if we connect



them with the Lower Palæozoic eruptions, as apparently Bertrand would do, they assume a different significance. In the former view they afford, as Geikie has remarked, a striking parallel with the great system of Tertiary dykes in the Inner Hebrides, the south of Scotland, and the north of Ireland. These dykes, it may be observed, are basic dykes, and in well-known cases, such as the lava-plains of the Snake River and the "Deccan traps," which seem to point to the tranquil welling out of large quantities of lava, these lavas are basaltic. Something of the same tendency may be observed in some large basalt-volcanoes of the ordinary type, such as those of Hawaii. Extravasation on a "plateau" scale is, however, by no means confined to basic lavas; witness, for instance, the highly acid rhyolites of the Yellowstone Park. In explosive eruptions of the most violent kind, on the other hand, the material seems to be in many cases of intermediate (andesitic) composition, Krakatau affording a memorable example. Other intermediate lavas, such as the often-described trachytes of Auvergne, occur in dome-like masses, as if when extruded they had been too viscid to flow away from the orifices that gave vent to them. These and other well-known facts, pointing apparently to some connection between what we may term the "habit" of lavas and their petrographical nature, belong rather to the branch of the subject to which we now proceed.

Coming then to more strictly petrographical considerations, the first thing to observe is that there exists a very sharply defined geographical distribution of groups of igneous rocks differing from one another in important chemical and mineralogical characteristics. To appreciate this we must recognise a broad two-fold division of the rocks as a whole. We are accustomed to speak of acid, intermediate, and basic rocks, etc., tacitly assuming that the rocks fall roughly into a linear series, such that, as the silica-percentage varies from one extreme to the other, the percentages of the other constituents vary as functions thereof. Though this is true to a certain extent, the variations actually shown by analyses of igneous rocks indicate a much higher degree of com-



plexity. A study of the practically infinite variety of rock-types met with in nature shows that we obtain a closer approximation to the truth by assuming two linear series instead of one. Each series bridges over the interval between the extreme acid and the ultrabasic rocks, and the two lines diverge most widely in the middle. They may be represented diagrammatically by two arcs meeting at either end. They are clearly traceable in either the volcanic or the plutonic division; the "dyke rocks," owing to the many peculiar types which arise as local differentiation-products, do not so readily fall into their places in this or any other scheme. To fix ideas we will take the lavas, regarding the rhyolites and the limburgites as the two extreme poles. To the one series belong the pantellarites, trachytes, phonolites and leucitophyres, nephelinites and leucitites, nepheline and leucite-basalts, and allied types; while the other includes the dacites, andesites and felspar-basalts. The leading chemical distinction lies in the behaviour of the alkalis, which in the former series increase in amount to a maximum and then fall off towards the basic end, while in the latter series they fall off steadily from the acid end to the basic. The difference is thus most marked in the intermediate members, the phonolites and allied rocks with 12 or 15 per cent. of alkalis presenting a strong contrast to the pyroxene-andesites with at most 5 or 6 per cent. This and some other differences in chemical composition naturally express themselves in the mineralogical constitution of the rocks, and most markedly so among those of mean silica-percentage. In the former series we not only find rocks composed mainly of alkali-felspars with little or no quartz, but minerals of the feldspathoid group (nepheline, leucite, sodalite, etc.), often figure largely, while the characteristic ferro-magnesian minerals are alkali-pyroxenes and alkali-amphiboles in contra-distinction to the common augites and hornblendes and the widely distributed rhombic pyroxenes of the rocks of the second series.

It has been remarked above that when a region of igneous rocks belonging to one great system divides into well-marked provinces, defined by their relations to axes of

folding, these provinces often differ from one another in respect of their petrographical characteristics. This is well seen in the light of the two-fold division of igneous rocks just enunciated, and the evidence is naturally clearest in the case of the Tertiary and post-Tertiary eruptions. Iddings has already drawn attention to the remarkable geographical distribution in the New World of the two petrographical series, which he names respectively the alkali and the sub-alkali group (4). Along, and to the west of, the great continental water-shed of the two Americas the vast areas of igneous rocks belong to the sub-alkali group. On the eastern slopes of the Rocky Mountains, however, in Montana, Wyoming, Colorado, and Texas, rocks rich in alkalies appear, and farther east numerous areas characterised by rocks of the alkali group occur in Canada, the New England States, New Jersey, and Arkansas, and in Brazil, Argentina, and Paraguay. Some of these rocks, it is true, are of pre-Tertiary age, and we probably have to deal with a case of the superposition of newer upon older provinces already alluded to. Apart from this question, however, we are justified in stating summarily that, of the latest great system of igneous rocks in America, the alkali and the sub-alkali groups are developed on the Atlantic and the Pacific slopes respectively.

In Europe the distribution of the two groups is equally clear, though not to be summarised in such simple terms. Judd long ago drew attention to the strong contrast between the Tertiary igneous rocks of Bohemia and those of Hungary, divided only by the Carpathian chain. The one set belongs to the alkali, the other to the sub-alkali group. Rocks of the former group are developed along the northern border of the Alpine zone of folding, from Bohemia to France, and in the Tyrrhenian province, while the rocks of the Hungarian, Servian, and Ægean provinces are relatively poor in alkalies. The Brito-Icelandic province, partly in consequence of the very sparing development of intermediate rock-types, is less sharply characterised. The rocks as a whole seem to belong decidedly to the sub-alkali group, though they are not without anomalies.



Farther south, however, in the Cape Verde Islands, Canaries, and Azores, we find rocks of the alkali-group, and again on the Atlantic coast of Africa. Rocks of the same group are recorded in various districts on the east coast of Africa, including Madagascar, and as far north at least as Massai Land and Kilimanjaro. On the other hand, almost the whole area of the Pacific Ocean and its borders seems to be characterised by sub-alkali rocks, though a few nepheline-basalts have been noted from some of the islands. Concerning the polar oceans our information is very incomplete. The elæolite-syenites and allied rocks of Greenland show that types rich in alkalies have at one time been well represented within the Arctic circle, and the little that is known of the petrology of the far south suggests the probability that the Antarctic is also an area of alkali-rocks. Leucite-bearing rocks are found even in New South Wales, though the age of these is not known, and they recur in Java and Celebes, coming there into close proximity with andesitic and other types belonging to the great Pacific region. The leucite-bearing rocks of Trebizonde appear at present to occupy an anomalous position.

If the distribution of the two groups of rocks thus briefly outlined be laid down in greater detail on a map and distinguished by different colours, a remarkable fact becomes apparent. This is the very general correspondence of the areas of the alkali and sub-alkali groups respectively with the areas of the Atlantic and Pacific types of coast-line as defined by Suess. The one type is found around the Atlantic and part of the Indian Ocean and in the Polar basins, the other, generally speaking, around the Pacific. Whether we may have to recognise an Atlantic and a Pacific facies of eruptive rocks, corresponding with distinct phases in crust-movements of a large order, is a question which it would be premature to answer at present; but it is at least clear that the distribution, not only of igneous rocks in general, but to some extent of different petrographical groups of rocks is in some way bound up with disturbances of the earth's crust or with the forces that



produce such disturbances. What is true of the Tertiary eruptions seems to be equally true of those belonging to earlier systems. Thus, in the Caledonian region, rocks of the alkali group occur in the Norwegian and of the sub-alkali group in the British province. The point has been touched upon in an earlier communication to this Journal,<sup>1</sup> and need not be pursued further.

Although what has been said would suggest that petrographical provinces may to some extent have been defined as such from the beginning, their individuality has become progressively more marked as the evolution of rock types proceeded, such evolution being advanced to different stages or following different lines in the several provinces of one region. The history of any one province during its period of life is also, from the petrographical point of view, a record of progressive specialisation, resulting in increasing diversity and peculiarity of rock types. In a typical province, conceived in the sense that we have indicated, the igneous rocks belonging to the earlier stages are often characterised by considerable uniformity and simplicity. Later a greater variety may be developed, sometimes running into highly specialised types, which do not readily find a place in any classificatory scheme. This seems to be the case especially in provinces belonging to the Atlantic facies, or in other words among rocks rich in alkalies. Specialisation is accompanied by localisation, and there may arise distinct districts having peculiarities of their own. Such a general law is not to be accepted without proper qualification; in particular we must suppose that the progress of evolution may be very unequal in different cases, and may be arrested by extinction of activity when only little advanced.

For illustration we recur to the Tertiary rocks of Pacific facies in America. Iddings has compared the lavas of the Andes with those of the Great Basin, between the Rocky Mountains and the Sierra Nevada (5). The former are almost exclusively andesites and dacites; the latter include similar types but, in addition, basalts and rhyolites.

<sup>1</sup> "SCIENCE PROGRESS," vol. i., pp. 152-165, 1894.

Iddings interprets this wider range of variety in the northern area as indicating that evolution is there in a more advanced stage than in the south. The province of the Andes, with its still active volcanoes, is in its youth; the Great Basin, where vulcanicity seems to be practically extinct, has reached middle or old age. Even in the latter case, however, the rocks evince no very high grade of specialisation, and the same types recur in different parts of the province. A strong contrast in these respects is presented by the rocks of the alkali group on the eastern slope of the "Great Divide," where, as Iddings has shown, both specialisation and localisation are carried to a high pitch.

A similar contrast is seen on comparing the intrusive rocks developed in the same provinces. It must be remembered that the earlier identifications of the igneous rocks of the Western states often require revision. Hague and Iddings have pointed out that many of the lavas named trachyte by Zirkel in Nevada and elsewhere are more correctly designated hornblende-pyroxene-andesite, and it does not appear that true trachytes have been identified west of the Rocky Mountains. The intrusive rocks which build the well-known laccolites of the Henry Mountains in Utah and similar masses in the West Elk, Mosquito, Abajo, La Sal, and other mountain groups of the high plateaux country have also been described in various places as trachytes. Whitman Cross in a recent memoir has shown that they have no right to this title, but are in general hornblende porphyrites (6). A very interesting point brought out by the author is the remarkable uniformity exhibited by the rocks of these great laccolitic intrusions over a tract extending from New Mexico northward through Utah and Colorado, and apparently at least as far as the borders of the Yellowstone Park. To this persistence of comparatively simple types of porphyrite and diorite throughout the High Plateaux and Great Basin tract are strikingly opposed the curious intrusive masses and complexes of Montana and other areas within and on the eastern edge of the Rocky Mountain belt, comprising augite and sodalite-syenites and theralites, with such peculiar modifications as the yogoite



and shonkinite of Weed and Pirsson, besides dykes of sölvbergite (the acmite-trachyte of Wolff and Tarr), Iddings' absarokite and allied types. Apart from the significance of the laccolitic habit, of which something may be said in a future number, the petrographical uniformity of the intrusions in the former case seems to connect itself with the geotectonic structure of the country in which they occur. If the physical process, whatever their nature, which give rise to diversity of intrusive rock-types stand related in some degree to mountain-building forces of the *horizontal* kind, a smaller range of varieties is to be expected in association with the monoclinal folds, normal faults, and other evidences of *vertical* movement which characterise what American geologists have styled the Great Basin type of mountain-structure. If this be so, we should look for a greater variety of intruded rocks in the true mountain tracts farther west. Concerning Tertiary intrusions in the Sierra Nevada there seems to be little information, but in the Coast Ranges of California the intrusive rocks presumably of this age include diabase, gabbro, peridotite, pyroxenite, and other types.

If highly specialised rock-types and very local distribution of the different types may be taken as the index of advanced evolution in a petrographical province, the Tyrrhenian province has arrived at a high stage of development. The assemblage of rock-types there belongs, as already remarked, to the alkali group. It is true that andesites occur among the earlier volcanic products of the Æolian Islands and again in the Cabo de Gata district, though some of the latter have unusual characters. The later lavas, however, throughout the province, cover a wide range of types, which for the most part carry a high content of alkalies. Some, such as the remarkable acid lavas of Pantellaria and the leucite-bearing rocks of Vesuvius, are unique and of strictly limited occurrence. Among active or recently active volcanoes we find some in close proximity to one another producing widely different lavas. Thus in the Lipari group the basalts of Stromboli are contrasted with the rhyolites of Vulcano, etc., and with the rocks of the

small island Vulcanello consisting, as Bäckström has recently shown, of leucite-basanite, though quite different from the Vesuvian lavas (7). The Etna basalts have a somewhat peculiar composition. Besides the augite-trachytes, some with sodalite, near Naples, and the more singular basic variety with olivine on Ischia, many curious trachytic rocks occur at various points from Monte Amiata in Tuscany to Monte Ferru in Sardinia. The Spanish and African parts of the province have been less completely investigated, but we may recall among the Cabo de Gata rocks the peculiar glassy lava with the composition of a lamprophyre, to which Osann has given the name *verite* (8).

The laws governing the local distribution of the several rock-types within such a province offer a problem on which as yet little light has been thrown. Lang has attacked it from the chemical standpoint, laying special stress upon the relative proportions of the alkalis and lime in the chemical analyses of the lavas and tuffs (9). He gives reasons for believing that the numerous volcanic centres in the neighbourhood of the Bay of Naples are situated on three main lines of fissure. The rocks in each set show a considerable range of composition, but have common characteristics in the respect indicated. One fissure or set of parallel fissures, which he calls the Appenine, runs parallel with the Appenine Chain to the Alban Hills and beyond. The other two, named the Pontine and the Tyrrhenian, take more westerly courses, crossing one another obliquely in the Ponza Islands. The fissures, the existence of which is thus inferred, are of course a different order of phenomenon from the dyke-fissures to which "massive" eruptions have been ascribed. If established, their different directions and the distinctness of the associated sets of rocks point to different dates for the activity of the several fissures. Indications of such fissures, or at least of secondary directing lines of volcanic activity, are to be discerned in other provinces; for instance, as Washington has shown in the *Ægean*; and they have been postulated by many writers on the phenomena of vulcanicity.

One feature which can scarcely be overlooked in the



most cursory view of the distribution of igneous rocks is the frequent association of widely different types in the same district or even at the same volcanic centre. Thus, among lavas, we often find rhyolites and basalts in intimate association; among dyke-rocks, aplite and minette, or bostonite and camptonite; among intrusions of more plutonic habit, granite or granophyre and gabbro. Such cases of what may be termed paragenesis are of too frequent recurrence to be regarded as fortuitous; the members of a pair must be "complementary" rocks, connected with one another by the ties of common origin.

Several writers have endeavoured to trace some law of general application in the succession in time of different types of igneous rocks in a district or province. Besides its obvious bearing upon genetic considerations, any such established order will tend to throw light upon many points touched upon in the foregoing paragraphs, such, for instance, as the association of particular rock-types with special habits of intrusion or with certain types of volcanic eruption. That the actual facts are far from simple is evident from the very different empirical results arrived at by different geologists. Thus Bertrand, from an examination of the history of igneous activity in the European area, lays down a general law of increasing basicity in the later products of each great system of eruptions; while Geikie, dealing more especially with the British Isles, finds in general evidence of increasing acidity.

Having regard to the volcanic rocks only, a succession which holds good in numerous districts, and has often been pointed out, is what may be described as an order of increasing divergence from an initial type. For instance, the earliest lavas or fragmental outbursts being of intermediate character, say, pyroxene-andesites, succeeding eruptions have been on the one hand increasingly acid, on the other increasingly basic, terminating perhaps with rhyolites and olivine-basalts. The two lines of variation have been in a general sense concurrent, and the order of precedence between corresponding terms of the two diverging series is not always the same. This succession was

first explicitly pointed out in the Western States, and it appears to hold not only in the Great Basin and on the High Plateaux but also in Mexico. Turner has shown, however, that the volcanic rocks of the Sierra Nevada district do not conform to this order, the earliest Tertiary eruptions being of rhyolite, followed by basalt, then by andesites, and finally by a later group of basalts (10).

Reviewing the history of volcanic eruptions at various periods, we find many cases which fall under the law of increasing divergence, and the number is considerably increased if we admit the possibility of reversion at a later stage to the original type, and again if we make allowance for the partial or total suppression of one of the diverging branches by the rocks of that branch being intruded instead of extruded. For instance, the Bala volcanic series of Carnarvonshire, beginning with some rocks of andesitic composition, consists mainly of a great succession of rhyolites, no basaltic lavas being developed. The basic branch, however, is sufficiently represented by innumerable intrusive sills of diabase associated with the lavas and by laccolitic intrusions of very basic hornblendic rocks at a lower horizon. Again, Geikie has pointed out the existence at the summit of the rhyolitic group of an andesite, constituting the latest volcanic outpouring in the district, and this may perhaps be regarded as marking a new accession of the original intermediate magma. Similar examples might be multiplied, but we also find many cases which cannot, without undue forcing, be brought under the law of increasing divergence, and we are bound to admit that any generalisation taking cognisance of the observed succession of volcanic rocks only is based on a partial view of the facts.

Some years ago Brögger established clearly the order of succession of the Devonian igneous rocks, mostly of plutonic and intrusive types, in the Christiania basin. It is in general an order proceeding from more basic to more acid, beginning with olivine-gabbro-diabase and passing through progressively more acid members to granite; but the latest rocks in the district are again basic. More recently the same



author has shown that the Triassic rocks of the Monzoni district present a rather close parallel to the Norwegian series, and he gives reasons for believing that the order of increasing acidity is one of wide general application, the final reversion to basic types being also of frequent occurrence though less characteristic (11). In many districts we find among true plutonic bodies of rock and their immediate offshoots evidence of basic eruptions having been succeeded by others of more acid composition, and sometimes a series of several terms showing progressively increasing acidity. Where, however, there has been a distinct later stage characterised by dyke intrusions, the order seems to have been often, if not generally, reversed, and the more basic dykes are seen to cut the more acid. These and kindred phenomena lead to theoretical considerations which will find their place more appropriately in a future communication. In what has now been written we have confined ourselves to remarks which are the direct outcome of observation and comparison.

ALFRED HARKER.

## RECENT WORK UPON VISCERAL AND ALLIED NERVES.

WITHIN the past few years our knowledge of the physiology and anatomy of the complicated tangle of nerve fibres and cells forming the sympathetic system has been making great advances; advances which are due to a very great extent to the active work of Langley and his co-workers, Dickinson and Anderson.

In the following account of our present knowledge of this subject I will first confine myself to the question of efferent fibres, leaving the discussion of the afferent fibres, upon which our knowledge is much scantier, for a later paper. Our proper appreciation of the true anatomical and physiological status of the sympathetic system may be said to date from 1885 when Gaskell's important paper on visceral innervation appeared in the *Journal of Physiology*.

For the purposes of this paper I have not referred back to earlier work than this, except in a few instances where it was necessary to make the account a little more complete. In most cases, however, the papers utilised have been published within the past five years. The whole has been divided up into sections, each giving an account for the different organs, and I have placed that for the pilo-motor nerves first as giving in many ways a more complete picture than any other, of the general arrangement of fibres and cells in the sympathetic system.

### PHILO-MOTOR NERVES.

The nerves which Langley and Sherrington have designated "pilo-motor," and which on stimulation cause contraction of the *erectores pilorum* and erection of the hairs, have been shown to form a constituent part of the sympathetic system.

Schiff<sup>1</sup> showed that electrical stimulation of the spinal

<sup>1</sup> Quoted by Langley, *Journ. of Physiol.*, vol. xv., p. 241, 1894.



cord caused erection of hairs in the tail, but that this effect disappeared after section of both lumbar sympathetic cords. Independently of this, and of one another, Langley<sup>1</sup> discovered that stimulation of the lumbar sympathetic in the cat caused erection of hairs, and Sherrington that stimulation of the cervical sympathetic in the monkey produced a similar effect. Starting with this as a basis Langley<sup>2</sup> has thoroughly worked out the course and distribution of these fibres, employing his results as a general indication of the arrangement of fibres of the sympathetic system.

He has shown that in the cat they arise from the cord in the anterior roots from the fourth thoracic to the third lumbar inclusive. In rare cases some were also found in the third thoracic and at times in the fourth lumbar, but, probably, only in the latter nerve, in those cats in which the arrangement of the lumbo-sacral plexus is posterior. These fibres leave the mixed nerve in its white ramus communicans and run to the corresponding ganglion, thus entering the sympathetic system. From these ganglia they may run upwards or downwards and ultimately leave in the grey rami to the various nerves and so reach the skin areas which they supply.

In a typical nerve all the pilo-motor fibres joining by its grey ramus pass into the posterior primary division of the nerve and are thus distributed to serial areas of the skin of the back which do not to any extent overlap one another.

This course was further examined to determine whether any nerve cells were interpolated on it. The method employed was that previously described by Langley and Dickinson,<sup>3</sup> who found that a solution of nicotine exerted a specific paralysing action on ganglion cells whether injected into the animal or applied locally, in 1 per cent. solutions, to the ganglion. After painting a ganglion with this solution he found that stimulation of the pilo-motor fibres running to this ganglion to leave it by its grey

<sup>1</sup> *Journ. of Physiol.*, vol. xii., p. 278, 1891.

<sup>2</sup> *Ibid.*, vol. xv., p. 176, 1894.

<sup>3</sup> *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889, and vol. xlvii., p. 379, 1889-90; *Journ. Physiol.*, vol. xi., p. 265, 1890.

ramus, almost without exception, produced no effect, though stimulation of the grey ramus produced the usual erection of hairs over its especial area of supply. Each pilo-motor fibre, therefore, leaves the cord in an anterior root and passes by the white ramus communicans of that nerve to the sympathetic system, and after a longer or shorter course ends in connection with a cell or cells in a sympathetic ganglion of the lateral chain. From this the impulses are carried by a fibre or fibres to the grey rami, and thence to their skin distribution. The ultimate distribution of the fibres in a white ramus usually does not in any way correspond to the distribution of the grey ramus running from that ganglion. Thus, for example, stimulation of the anterior roots of the eleventh thoracic nerves after previous ligature and section produced erection of a longish strip of hairs in the lumbar region, whilst stimulation of the grey ramus of that nerve produced energetic erection of hairs in a short strip a little distance above the long strip, and separated from it by a quiescent region. The areas supplied by successive anterior roots are found to form successive strips which, however, frequently overlap one another to a considerable extent. Langley<sup>1</sup> found that stimulation of an anterior root with weak shocks produced an erection of hairs supplied by all the fibres issuing by that root. Then if the strength of the stimuli be considerably increased in addition to the first effect, an erection of hairs in a narrow strip supplied by the grey ramus running to that nerve is now produced. The first effect is obliterated on paralysing the ganglion cells by injection of nicotine whilst the latter effect is of course unaffected.

In the monkey, Sherrington showed that the pilo-motor fibres found in the cervical sympathetic left the cord by the second to the sixth thoracic nerves, and had ganglion cells upon their course in the superior cervical ganglion. Thence they are distributed to the hair on the forehead, front of scalp, temple, cheek and the upper part of the whisker.

<sup>1</sup> *Loc. cit.*, p. 203.



In the cat, Langley found that the similar fibres leave the cord from the fourth to the seventh thoracic nerves—on rare occasions by the third as well—and thus reach the superior cervical ganglion, where nerve cells are interpolated on their course. The grey rami to the first, second and from the ganglion and supply two regions—(i.) a “face third cervical nerves and the cranial rami carry the fibres area,” between the eye and the ear, supplied by the latter; and (ii.) a dorsal strip extending from just behind the anterior level of the ears to, as a rule, some point over the fourth vertebræ.

The next set of nerve fibres have their cells in the ganglion stellatum. These leave the cord in the fifth to eighth thoracic nerves, and from the ganglion are distributed by a vertebral ramus to the third to eighth cervical nerves and supply a dorsal strip extending from the fourth cervical vertebra to the front of the third thoracic vertebra. This strip is narrow above and broadens out below. The ganglion stellatum also sends pilo-motor fibres by its grey rami to the first, second, third and fourth thoracic nerves. These supply areas roughly corresponding to one vertebra each, and thus extend from the third to the seventh or even eighth thoracic vertebra.

For the remaining ganglia of the chain, the fibres leave the cord from the seventh thoracic to the third or fourth lumbar nerve inclusive. The third is usually the last, and supplies fibres to the parts from the anus to the tip of the tail. As a rule, the nerve cells for these pilo-motor fibres are in the ganglia, from which they are given off to the spinal nerves, though occasionally in the lumbar region, they are placed in the ganglion immediately above. Each grey ramus supplies the skin over about one vertebra. Thus the grey ramus to the fourth lumbar nerve supplies the hairs over the seventh lumbar vertebra and sacrum. There is a curious gap in the distribution to grey rami, for usually that to the sixth lumbar nerve contains no hair fibres. There is, however, no gap in the skin distribution, and the first sacral grey ramus follows the lowest effective lumbar ramus. The first effective ramus below the in-

effective lumbar ramus or rami supplies a strip of skin immediately below the sacrum.

The second sacral supplies the hairs dorsal to the anus; the third, those about one inch below the anus; and the coccygeal, the remainder to the tip of the tail.

Now, by a comparison of the full areas supplied by the anterior spinal roots with the areas of the grey rami, the accurate connection of any anterior root with the ganglia, or conversely of any ganglion with the anterior roots, can be determined; and Langley, in his later paper, gives a series of tables<sup>1</sup> in which this has been done.

In a few experiments on the dog, Langley found that the general arrangement of these fibres is the same as in the cat.

Where, as is usually the case in tracing the course of these sympathetic fibres, we find that their path is made up of two segments, each consisting of a nerve cell and its fibre, the upper fibre whose cell is placed in the spinal cord and which terminates in dendrites in one or other of the ganglia of the system is termed by Langley the præ-ganglionic fibre. The other fibre, whose cell is placed in the ganglion and whose fibre runs, as a rule, to the nerve-ending in the organ, he terms the post-ganglionic.

In considering, moreover, the origin of the different fibres in the lumbar region, there are other points of nomenclature adopted by Langley which are of great importance. As the number of thoracic and lumbar nerves is very variable, and as the first sacral is a nerve which is always readily distinguished from all others, he starts with this as his fixed nerve. The immediately preceding seven nerves are called the first, second, etc., lumbar nerves successively.<sup>2</sup> If there is another lumbar nerve above that, it is termed the extra lumbar. Sometimes, moreover, the seventh nerve above the first sacral has a small rib, but this he still terms the first lumbar nerve.

Langley<sup>3</sup> also describes the lumbo-sacral plexus of the

<sup>1</sup> *Loc. cit.*, pp. 220, *et seq.*

<sup>2</sup> See Langley, *Journ. of Physiol.*, vol. xvii., p. 297, 1894-5.

<sup>3</sup> *Loc. cit.*, p. 296.



cat as presenting several variations. These he divides into three chief groups called respectively anterior, median, and posterior. "The simplest method of distinguishing these classes is to note the relative size of the strands to the sciatic furnished respectively by the sixth lumbar and by the upper branch of the first sacral. If the former is distinctly larger than the latter, the plexus belongs to the anterior class; if the two are of about the same size, the plexus is median; if the strand from the first sacral is distinctly larger than that from the sixth lumbar, the plexus is of the posterior class."

#### VASO-MOTOR NERVES.

Gaskell,<sup>1</sup> in his important paper upon visceral and vascular nerves, deals with the question of the course and distribution of the two sets of vaso-motor nerves. The method he employed was to a large extent an anatomical one. He showed that the visceral fibres present in any root may all be traced into the white ramus communicans of that root, because their transverse diameter is much smaller than the average diameter of the ordinary sensory and motor fibres of the two roots. He concludes that vaso-constrictor nerves for all parts of the body are restricted to the anterior roots of the spinal nerves between the second thoracic and fourth lumbar inclusive, whence they pass as medullated nerves to the ganglia of the main sympathetic chain, from which they issue as non-medullated nerves and pass to their destination. For vaso-dilator nerves, he shows that some leave by the cervico-cranial and sacral sets of visceral nerves; but whether there are more from other roots he does not decide.

*To the Trunk and Limbs.*—By recording plethysmographically the variations in volume of the limbs and the general blood pressure simultaneously, Bradford and Bayliss<sup>2</sup> have examined the origin of the constrictor nerves to the limbs. For the fore-limb in the dog, they find constrictor

<sup>1</sup> *Journ. of Physiol.*, vol. vii., p. 1, 1885-6.

<sup>2</sup> *Ibid.*, vol. xvi., p. 10, 1894.

fibres issuing by the third to eleventh thoracic inclusive, but chiefly by the fifth to ninth inclusive. For the hind limb, from the eleventh thoracic to third lumbar inclusive, mainly however in the twelfth thoracic to second lumbar inclusive.

Langley<sup>1</sup> finds that the fibres for the upper limb terminate in the cells of the ganglion-stellatum; those for the hind limb in cells in the sixth and seventh lumbar and first sacral ganglia. The fibres issuing from these cells run chiefly into the corresponding grey ramus, but in a few cases may run down the sympathetic chain and issue by the grey ramus of the next ganglion. Langley,<sup>2</sup> in a later paper on the constrictor supply to feet of the cat, shows that they leave the cord in the fourth to ninth thoracic nerves inclusive for the fore foot; and to the hind foot in the twelfth thoracic to third lumbar nerves with an anterior plexus, or in the twelfth thoracic to fourth lumbar with a posterior plexus. On the whole, the two results agree when we remember that Bayliss and Bradford's experiments were performed upon the dog, and involved the larger part of the limb, and that Langley's observations were made on the cat, and were restricted to the vessels of the feet.

E. Cyon,<sup>3</sup> in 1868, by studying the effects upon the temperature of the limb after section of the sympathetic cord in various positions, and of the lower cervical and upper dorsal rootlets, concluded that the vaso-constrictor fibres for the upper limb leave the cord through the mid-dorsal roots, thence travel to the ganglion-stellatum, and so by its rami reach the cords of the brachial plexus.

With regard to the vaso-motor fibres to the trunk, Langley<sup>4</sup> finds that, in the main, they are the same as the origin of the pilo-motor fibres, though their distribution for any particular ramus is as a rule rather more extended than that of the latter from the same ramus.

<sup>1</sup> *Journ. of Physiol.*, vol. xii., p. 373, 1891.

<sup>2</sup> *Ibid.*, vol. xvii., p. 307, 1894-5.

<sup>3</sup> *Leip. Ber.*, vol. xx., p. 73, 1868.

<sup>4</sup> *Loc. cit.*, p. 312.



The pre-ganglionic vaso-motor nerves to the tail<sup>1</sup> leave the cord by the third and fourth lumbar nerves and to a less extent by the second lumbar. By nicotine it is shown that these fibres are connected with cells in the coccygeal ganglia.

*To the Head.*—The pre-ganglionic fibres constricting the vessels of the head,<sup>2</sup> in the cat and dog, leave in the first to fifth thoracic anterior roots inclusive, but chiefly in the second, third and fourth. They terminate in cells in the superior cervical ganglion.<sup>3</sup> Certain fibres causing dilatation of the vessels in the gums and lips in the dog, have also been shown by Langley and Dickinson to be connected with cells in the superior cervical ganglion.<sup>4</sup>

*To the Brain.*—Roy and Sherrington,<sup>5</sup> in a paper dealing with the general physics of the circulation in the brain, were unable to gain any satisfactory evidence of vaso-motor fibres to the cerebral vessels in the nerves of the neck, “and that therefore there is no evidence of their existence outside the cerebro-spinal canal”. Bayliss and Hill<sup>6</sup> have also carried out many experiments with the aim of determining the presence of these vaso-motor fibres, but again with negative results.

The course of efferent fibres from the cord is almost universally considered as through the anterior roots, and so general is this that any statement of the presence of efferent fibres in the posterior roots should be most critically examined. In 1876 Stricker<sup>7</sup> described his experiments and results upon the vascular nerves in the sciatic. His method was by thermometric observation of the foot after section or stimulation of the nerves in different parts of their course. He describes the posterior roots of the fourth and fifth lumbar nerves of the dog as always containing vaso-dilator

<sup>1</sup> Langley, *loc. cit.*, p. 311.

<sup>2</sup> Langley, *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.

<sup>3</sup> Langley and Dickinson, *Proc. Roy. Soc.*, vol. xlvii., p. 379, 1889-90.

<sup>4</sup> See also Langley, *Journ. of Physiol.*, vol. ii., p. 146, 1890.

<sup>5</sup> *Journ. of Physiol.*, vol. xi., p. 85, 1890.

<sup>6</sup> *Ibid.*, vol. xviii., p. 334, 1895.

<sup>7</sup> *Sitz. d. k. Ak. d. Wiss. Wien*, vol. lxxiv., iii., p. 173, 1876.

fibres which run directly into the sciatic. The constrictor fibres are situated in the lower thoracic and upper lumbar and pass through the sympathetic chain. The presence of these fibres in the posterior roots has given rise to much discussion. Stricker's results were confirmed by Gärtner, but denied by Vulpian, Cossy, etc. Of recent workers Morat<sup>1</sup> cannot confirm the presence of these fibres, but on the other hand Hasterlik and Biedl<sup>2</sup> confirm Stricker's experiments. In this connection we find anatomical evidence of the presence of fibres in the posterior roots which have the characters which are usually regarded as typical of efferent fibres. Ramon-y-Cayal<sup>3</sup> describes fibres passing through the posterior roots and without branching going straight to the anterior horn, where they end in nerve-cells. v. Lenhossek<sup>4</sup> also describes similar fibres and cells—the fibres passing through the posterior root ganglion without becoming connected with cells in that ganglion. Lastly v. Gehuchten<sup>5</sup> finds similar cells in his examination of the spinal cord of the fowl at early stages of development.

Werziloff<sup>6</sup> has recently published further experiments in this direction. He employed for his experiments large dogs which were curarised and under chloroform. His methods were two in number; either to examine temperature changes as each posterior root was cut, or to place the hinder leg in a plethysmograph and so obtain tracings of the changes in volume. He describes very positive evidence of vaso-dilator fibres in the sixth and seventh lumbar, and first sacral posterior roots for the foot and similar fibres, though less numerous, in the fourth and fifth lumbar for the upper part of the leg and lower part of the thigh.

Gaskell<sup>7</sup> especially examined the posterior roots of the first, second and third sacral for the presence of vaso-dilator

<sup>1</sup> *Arch. de Physiol.*, vol. xxiv., p. 689, 1892.

<sup>2</sup> *Wiener. klin. Wochenschr.*, p. 43, 1893.

<sup>3</sup> *Anat. Anz.*, vol. v., p. 112, 1890.

<sup>4</sup> *Ibid.*, p. 360, 1890.

<sup>5</sup> *Ibid.*, vol. viii., p. 215, 1893.

<sup>6</sup> *Centr. f. Physiol.*, vol. x., p. 194, 1896.

<sup>7</sup> *Journ. of Physiol.*, vol. viii., 1887; *Proc. Physiol. Soc.*, p. 4.



fibres running into the nervi erigentes, but never found them (rabbits). They always passed through the second and third anterior roots.

*To the lungs.*—Bradford and Dean<sup>1</sup> describe vaso-constrictor fibres to the pulmonary vessels as occurring in the anterior roots of the third, fourth and fifth thoracic nerves and to a less extent in the sixth and seventh. They experimented upon dogs, taking simultaneous tracings of the variations of pressure in the pulmonary artery and carotid. Their results have been confirmed by François Franck.<sup>2</sup> He criticised their method as not being the best, and liable to introduce factors difficult to interpret. He therefore took simultaneous pressure tracings of the pulmonary artery and left auricle, and required as a test for constriction of the pulmonary artery a simultaneous rise of pressure in the artery, with a fall in the auricular pressure. In this way he finds that the constrictors are chiefly placed in the second and third thoracic nerves, and that none are found below the fifth and sixth.

With regard to the origin and distribution of the vascular nerves to other organs, it will be more convenient to state what is known of them when discussing the general nerve supply of each organ. In this way we shall save repetition. for the origin of the vascular nerves is the same, as a rule, as that of the visceral fibres.

#### THE CARDIAC NERVES.

The *accelerator* nerves, as Langley<sup>3</sup> has shown, leave the cord chiefly by the second and third thoracic roots, to a less extent in the fourth thoracic, and to a much slighter extent in the first and fifth thoracic. It is indicated by a few experiments, though not conclusively proved, that the cells on the course of these fibres lie in the ganglion stellatum and inferior cervical ganglion. The experiments were carried out on cats. The spinal origin of these fibres is confirmed for the dog by Bayliss and Starling.<sup>4</sup>

<sup>1</sup> *Journ. of Physiol.*, vol. xvi., p. 34, 1894.

<sup>2</sup> *Arch. de Physiol.*, vol. xxvii., pp. 744 and 816, 1895.

<sup>3</sup> *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.

<sup>4</sup> *Journ. Physiol.*, vol. xvii., p. 126, 1894.

The *inhibitory* fibres of the vagus have also had their origin and cell-connections investigated. Grossmann<sup>1</sup> examined the rootlets of the ninth, tenth and eleventh cranial nerves to determine in which of these rootlets the inhibitory fibres left the medulla. For purposes of reference he divides the rootlets into the three groups as they are anatomically arranged; these groups he speaks of as group (*a*), (*b*) and (*c*) respectively. The fibres of group (*a*) correspond fairly well, though by no means entirely, with the fibres forming the glosso-pharyngeal, group (*b*) with the vagus, and group (*c*) with the medullary origin of the spinal accessory. He examined each of these rootlets as they leave the medulla, employing rabbits as the animals experimented upon, for cardio-inhibitory nerves by unipolar stimulation of each rootlet immediately as it arose from the medulla, after cutting it through close to its origin or after tearing it from the medulla. He found them in the lower two or three rootlets of group (*b*) and the upper rootlet of group (*a*). F. Vas<sup>2</sup> has also examined these same rootlets in the skull cavity for their effect upon the heart. He tears through the rootlets and notes the effect upon the heart and upon the blood pressure. He does not find any cardiac nerves in the accessory rootlets. With regard to the further connections of these fibres Gaskell<sup>3</sup> showed that in the crocodile and alligator, by the degeneration method, these fibres had no connection with cells in the ganglion trunci, but were continued straight down as medullated fibres to their termination in the heart substance, where their endings were probably in relation with some of the cardiac ganglion cells. This connection of the fibres with intrinsic cardiac ganglia is shown by the action of nicotine applied locally to the heart.<sup>4</sup> After the application of nicotine the heart can no longer be inhibited by stimulation of the vagus in the neck, though it can if the fibres in the substance of the heart be stimulated. The vagus fibres

<sup>1</sup> *Pflüger's Archiv*, vol. lix., p. 1, 1894.

<sup>2</sup> *Ungar Arch. f. Med.*, iii., 1894.

<sup>3</sup> *Journ. of Physiol.*, vol. vii., p. 22 *et seq.*, 1885-6.

<sup>4</sup> See Langley and Dickinson, *Journ. of Phys.*, vol. xi., p. 279, 1890.



therefore from their medullary origin to their termination in the intrinsic ganglia form the præ-ganglionic fibres, from the ganglion cells to the heart muscle terminals the post-ganglionic. This double segmentation is also confirmed by a degeneration method by Nikolajew.<sup>1</sup>

#### INNERVATION OF THE MUSCULAR WALLS OF THE ALIMENTARY CANAL.

*Œsophagus.*—It has long been known that peristaltic contractions of the œsophagus may be produced by stimulation of the vagus either in the neck or thorax. Gaskell<sup>2</sup> investigated the function and course of these fibres, choosing crocodiles and alligators for his experiments, because in these animals the two vagal ganglia, ganglion jugulare and ganglion trunci, are separated by the whole of the cervical portion of the vagus. Stimulation of the nerve in the crocodile either above or below the ganglion trunci produced a strong peristaltic contraction of the œsophagus extending through both the cervical and thoracic portions and ending in a contraction of the stomach. In the alligator the course of the fibres is a little different, those for the thoracic portion running as in the crocodile, whilst the fibres for the cervical portion “pass directly to it probably by way of the large conjoint vagus and glossopharyngeal ganglion and the pharyngo-laryngeal nerve.

The presence of nerve cells on the course of these fibres was next investigated by removal of a piece of the vagus in the neck and observation of the effects of stimulation of the nerve above and below the ganglion trunci. It was thus proved that the motor fibres for the thoracic portion of the œsophagus have nerve cells interposed upon their course, and that these cells are situated in the ganglion trunci. In the crocodile the fibres for the cervical portion of the œsophagus pass through the ganglion without coming into connection with the nerve cells. These fibres above the ganglion are fine medullated fibres, whereas below the ganglion they are found to be non-medullated.

<sup>1</sup> *Arch. f. (Anat. u.) Physiol.*, suppl., p. 67, 1893.

<sup>2</sup> *Journ. of Physiol.*, vol. vii., p. 19, 1886.

Kreidl<sup>1</sup> has examined the roots of the glossopharyngeal, vagus and accessory at their exit from the medulla to determine in which rootlets these fibres leave the central nervous system. These roots are described by Grossmann<sup>2</sup> as arranged in three groups, which, for convenience of description, he speaks of as group (*a*), group (*b*), and group (*c*). Group (*a*) corresponds chiefly to the glossopharyngeal, (*b*) to the vagus, and (*c*) to the spinal accessory.

Kreidl's method consists in dividing one or more of these roots at their exit from the medulla without anæsthetics and shortly after they have been given a meal consisting of green food-stuffs. The animals (rabbits) are then allowed to recover and given a meal of carrots. In those experiments in which the roots of either groups (*b*) or (*c*) had been divided no paralysis of the œsophagus was observed, but where group (*a*) had been divided the animal soon ceased to eat and the œsophagus was found full of food. This result was constant in over thirty rabbits. He further shows that section of the glossopharyngeal immediately after it leaves the cranium has no influence over the result, and that consequently the fibres after passing through the roots of group (*a*) pass directly into the vagus.

Steinach<sup>3</sup> states that in the frog not only does the vagus contain motor fibres for the œsophagus, but that similar ones are present in the *posterior* roots of the second and third nerves.

Réthy<sup>4</sup> by stimulation of the peripheral end of these roots concludes that the fibres for the tensor palati leave in the motor root of the fifth, for the stylo-pharyngens in group (*a*) and for the constrictors of the pharynx, the levator-palati, the palato-pharyngeus, and the palato-glossus in group (*b*).

*Stomach.*—In a paper upon the peristaltic contraction of the stomach and intestines, which contains an account of

<sup>1</sup> *Pflüger's Archiv*, vol. lix., p. 9, 1895.

<sup>2</sup> *Ibid.*, p. 1, 1895.

<sup>3</sup> *Ibid.*, vol. lx., p. 593, 1895.

<sup>4</sup> *Sitz. d. k. Ak. Wien*, vol. ci., Abt. iii., p. 381, 1892.



the earlier literature, Houckgeest<sup>1</sup> confirms and extends previous observations upon the innervation of the stomach. He concludes that both right and left vagi contain fibres stimulation of which leads to an increase in the movements of the stomach, and that the two splanchnics contain inhibitory fibres to the stomach muscles.

Openchowski<sup>2</sup> in two papers describes the results of his experiments upon the central and peripheral innervation of the stomach. His method consists of the introduction of a sound carrying an elastic bag into the stomach. The bag is brought into different positions in the pylorus, the cardiac orifice or the cavity of the stomach, and by being connected with a recording tambour tracings of the movements of the different parts may be obtained. He concludes that the different parts possess a power of rhythmic contraction which, however, is modified by nervous impulses reaching it from the brain or cord. For the cardiac orifice there are two sets of fibres, one set opening the other closing the orifice. The latter he describes as passing from a centre in the region of the posterior corpus quadrigeminum by two different paths. The first and chief one is *via* the vagus, especially the left, the second down the cord and out by the anterior roots of the fifth to eighth thoracic nerves inclusive, and thence by the splanchnics to the stomach. The fibres, stimulation of which leads to the opening of the cardia, he describes as passing either down the vagus or along the cord, to issue by the upper thoracic nerves as low as the fifth and thence by the splanchnics, especially the smaller. For the pyloric orifice the constrictor fibres pass along the vagus and the dilator fibres pass down the cord and leave it in the anterior roots of the thoracic nerves above the tenth. He states that, in the rabbit, there are more excito-motor fibres than inhibitory in the splanchnic, whereas in the dog the reverse is the case.

<sup>1</sup> *Pflüger's Archiv*, vol. vi., p. 266, 1872.

<sup>2</sup> *Arch. f. Anat. u. Physiol.*, p. 549, 1889, and *Centralblatt f. Physiol.*, vol. iii., p. 1, 1889.

Langley and Dickinson<sup>1</sup> found that in the dog or cat stimulation of the vagus caused movement of the stomach and stimulation of the splanchnic inhibited that movement.

Oser<sup>2</sup> examined the innervation of the pylorus by observation of its condition through an opening in the duodenum either by means of a cylindrical rubber bag passing through it, or by simply passing a finger through it and noting the resistance offered. He found that stimulation of the vagus markedly increased that resistance and stimulation of the splanchnic had the reverse effect. By introducing a sound and filling the stomach with warm saline solution after the duodenum had been occluded by a ligature below the pylorus he showed that stimulation of the vagus produced a marked contraction which was followed after the cessation of the stimulus by a relaxation to a greater extent than before stimulation. Stimulation of the splanchnic produced cessation of any irregular rhythmic contractions that might have been present, accompanied by a relaxation. On cessation of the stimulation, the tonic contraction increased and was accompanied by an unusually active rhythm which however is easily inhibited by renewed splanchnic stimulation. His experiments were carried out upon dogs.

Morat<sup>3</sup> investigated the movements of the stomach by introducing a sound carrying a thin-walled bag into the empty stomach. The bag can then be distended to a certain extent and registers the movement of the stomach-wall. He describes a marked rhythm which varies very much in different cases, but increasing in rate, in force and in tone, on stimulation of the peripheral cut end of either vagus. Stimulation of the splanchnic brings about the reverse effect, *viz.*, a diminution in the amount of tone, and a fall in the rate and force of the rhythm. He moreover found evidence of muscular inhibitory fibres in the vagus, for he found that stimulation of the central end of one divided vagus, the opposite being intact, produced a dilation of the organ which dilatation was not produced if the

<sup>1</sup> *Proc. R. S.*, vol. xlv., p. 423, 1889.

<sup>2</sup> *Zeitschr. f. klin. Med.*, vol. xx., p. 285, 1892.

<sup>3</sup> *Arch. de. Physiol.*, vol. xxv., p. 142, 1893.



opposite vagus was cut. Doyon<sup>1</sup> confirms this result and adduces further evidence of the presence of these inhibitory fibres in the vagus, for he finds that after the injection of pilocarpine the first effect of stimulation of the vagus is to produce dilatation which is later followed by the usual contraction. The injection of strychnine in suitable doses gives practically the same result.

Contejean<sup>2</sup> experimenting on frogs and toads describes the vagus as carrying motor fibres to the general stomach wall and to the cardiac and pyloric sphincters, and in addition fibres inhibiting movements of the sphincters. By a weak stimulation inhibitory effects are produced; with strong stimulation energetic contraction of the cardia and pylorus, then of the longitudinal fibres and finally peristalsis; stimulation of the sympathetic, or better of the cœliac plexus, leads to contraction of the circular fibres, but not peristalsis. If in a curarised frog water be placed in the mouth after both vagi are cut this is not driven into the stomach, and the cardiac orifice shows marked rhythmic contractions, thus illustrating the absence of the usual inhibitory effects. If, on the other hand, both vagi be cut in a non-curarised frog the results obtained are due to a failure of the usual motor effects, *e.g.*, air taken into the mouth is driven into the stomach as well as into the lungs.

Doyon<sup>3</sup> has examined the innervation of similar parts in pigeons and fowls. The crop is a part of the œsophagus and is innervated in a similar manner to it. The gizzard and proventriculus show rhythmic contractions which are increased in number and in rate by vagal stimulation and also increased in tonus. Stimulation of the splanchnic arrests rhythmic movements if these be present, but if the organs be at rest it may produce a single contraction. Stimulation of the central end of the vagus the other being intact causes relaxation of the gizzard and proventriculus, an effect which is abolished by section of the opposite vagus. Pilocarpine

<sup>1</sup> *Arch de Physiol.*, vol. xxvii., p. 374, 1895.

<sup>2</sup> *Comp. Rend.*, vol. cxiii., p. 150, 1891, and *Arch. de Physiol.*, vol. xxiv., p. 640, 1892.

<sup>3</sup> *Arch. de Physiol.*, vol. xxvi., p. 887, 1894.

causes contraction of the crop, gizzard and proventriculus, and if while these parts are thus firmly contracted the vagus be stimulated, a dilatation of the gizzard and proventriculus is produced. In these two ways then the presence of inhibitory fibres in the vagus is demonstrated.

With regard to the presence of nerve cells upon the course of these fibres, Gaskell<sup>1</sup> showed in his experiments upon alligators and crocodiles that the fibres for the stomach contained in the vagus were connected with nerve cells in the ganglion trunci vagi, and that here too they became non-medullated.

Langley and Dickinson<sup>2</sup> have further shown that the inhibitory fibres contained in the splanchnic terminate in cells in the coeliac ganglion, and that the motor fibres of the vagus do not become connected with cells in the solar plexus or its immediate offshoots. After painting the coeliac plexus with nicotine the rhythmic movements of the stomach are greatly increased, and stimulation of the splanchnic no longer interferes with that rhythm. Steinach<sup>3</sup> describes motor fibres for the stomach of the frog in the vagus, and also in the posterior roots of the third and fourth spinal nerves.

*Small Intestine.*—It has been commonly stated that the arrangement of the double nerve-supply of the small intestine is that the one set, vagus fibres, cause contraction of the circular and inhibition of the longitudinal fibres, the second set, splanchnic fibres, cause contraction of the longitudinal and inhibition of the circular fibres. The view that the general function of the vagus is excito-motor and of the splanchnic inhibitory appears however to be the one which results from the experiments of most later observers, though at times the splanchnic may give rise to contractions but not of the ordinary peristaltic character. These irregular contractions caused by stimulation of the splanchnic may well be due to secondary effects brought about by the constricting influence which the nerve exerts over the blood-vessels.

Houckgeest<sup>4</sup> in his experiments upon peristalsis con-

<sup>1</sup> *Loc. cit.*

<sup>2</sup> *Loc. cit.*

<sup>3</sup> *Loc. cit.*

<sup>4</sup> *Loc. cit.*



firms the fact that vagus stimulation increases the peristaltic contractions more especially after previous section of the two splanchnics. That the splanchnic contained inhibitory fibres he considered was to be deduced from the marked increase in peristaltic activity consequent upon their section.

Langley and Dickinson<sup>1</sup> obtained marked increase of peristaltic movements on stimulation of the vagus, an increase which was quickly inhibited by stimulation of the splanchnic. Pal and Berggrün<sup>2</sup> showed that the effect of the vagus could be very largely increased if before stimulation the cord be cut in the neck or a transverse section of the brain be made at the pulvinar or anterior third of the optic thalamus, and concluded that inhibitory fibres passed through the parts cut. Pal<sup>3</sup> showed that many of the irregular results obtained in experiments upon the muscular movements of the intestines were due to their exposure to the air. He observed the movements through the abdominal wall after this had been shaved, and found that on stopping artificial respiration in curarised dogs or rabbits these movements were greatly increased, an increase which was not abolished by section of both vagi, though the contractions could be made much more vigorous by stimulation of either vagus. On opening the abdomen the movements quickly ceased, and a second stimulation of the vagus produced either no effect or only a weak contraction. Moreover on now stopping artificial respiration the peristalsis which was so marked when the abdomen was intact no longer occurred. He also adduces experiments<sup>4</sup> to show that in addition to the ordinary splanchnic centre there is another placed lower down in the cord which inhibits peristalsis. His statement is general, not limited to the lower part of the small intestine or to the large intestine. Jacobi<sup>5</sup> examined the movements of the intestine in animals in which the intestines were exposed under warm

<sup>1</sup> *Proc. Roy. Soc.*, vol. xlv., p. 423, 1889.

<sup>2</sup> *Wien med. Jahrb.*, p. 434, 1888.

<sup>3</sup> *Arb. a. d. Inst. f. alg. u. exper. Path. Wien*, p. 31, 1890.

<sup>4</sup> *Wiener. Klin. Wochenschr.*, pp. 199, 521, 1895.

<sup>5</sup> *Arch. f. exp. Path. u. Pharm.*, vol. xxix., p. 171, 1892.

saline solution, and confirmed the ordinary effects of vagus and splanchnic, finding, however, that the vagi usually had unequal actions, sometimes the left sometimes the right producing greater peristalsis. Bechterew and Mislawski<sup>1</sup> experimented with the object of determining the roots by which the fibres in the splanchnic innervating the small intestine left the cord. They found them in the anterior roots of the sixth thoracic to first lumbar inclusive.

Langley and Dickinson<sup>2</sup> showed that painting the superior mesenteric ganglion with nicotine abolished the effect of splanchnic stimulation, and that the motor fibres of the vagus do not end in cells of the solar plexus. Further, Gaskell<sup>3</sup> showed by the method of degeneration that in all probability the motor fibres of the vagus are connected with cells in the ganglion trunci vagi.

We may therefore sum up our knowledge of the muscular innervation of the small intestine in the following way :  
fine?
 (1) A set of ~~five~~ medullated fibres leave the medulla in the vagal rootlets, are connected with cells in the ganglion trunci, and then continue as non-medullated fibres straight to the intestinal walls, passing through the solar plexus but not being connected with cells in that plexus. Stimulation of this set causes contraction of both the longitudinal and circular coats. (2) A set of fine medullated fibres arise from the cord, leave by the anterior roots from the sixth thoracic to the first lumbar inclusive, pass through the lateral chain of ganglia and are connected with cells placed chiefly in the superior mesenteric ganglia. Thence they are traced as fine non-medullated fibres to the muscular coats. Stimulation of these fibres causes inhibition of any peristaltic movements that may be present. At times stimulation has been noted to cause an isolated contraction, often local and of a non-peristaltic nature, a contraction which may most reasonably be accounted for as an effect secondary to the contraction of blood-vessels, simultaneously caused by the stimulation.

<sup>1</sup> *Arch. f. (Anat. u.) Phys.*, suppl., p. 243, 1889.

<sup>2</sup> *Loc. cit.*

<sup>3</sup> *Journ. of Phys.*, vol. vii., p. 19, 1886.



According to Steinach, the upper part of the small intestine of the frog receives motor fibres through the posterior roots of the fourth and fifth nerves, the lower part through the fifth and sixth.

*Vaso-motor Nerves to the Intestines.*—The course of the vaso-constrictors to the stomach and small intestine has long been known to be by the splanchnics. Langley and Dickinson<sup>1</sup> showed that their course was interrupted by nerve cells which were placed in the cœliac or superior mesenteric ganglia. Painting the ganglia with nicotine abolishes the usual effect on the blood pressure, of stimulation of the splanchnic. The local application of nicotine to the ganglia causes first a rise in blood pressure, stimulating action on the nerve cells, followed by a marked fall as the cells become paralysed. In a recent paper, Langley<sup>2</sup> gives further evidence of the position of the cells on the course of the vascular fibres to the intestine. After a sufficient dose of nicotine, the marked rise in blood-pressure consequent on stimulation of the splanchnic is abolished, but stimulation of the nerves leaving the solar plexus can still produce the usual rise in blood-pressure. He concludes that there is one, and only one, cell station on any vaso-constrictor nerve. Contejean,<sup>3</sup> for the frog, describes both vaso-dilators and constrictors as occurring in the vagus, the dilators being present to the greatest extent. The main number of the constrictors reach the organ by the sympathetic chain.<sup>4</sup> Hallion and François Franck<sup>5</sup> have recently published some experiments upon the origin and course of these nerves. Their method is a plethysmographic one and consists in enclosing one or more loops of the intestine in a glass vessel in which it is covered by warm saline solution. The upper orifice is closed by an air-tight lid, and changes in pressure of the air imprisoned over the salt solution are recorded by means of a sensitive

<sup>1</sup> *Proc. Roy. Soc.*, vol. xlv., p. 423, 1889.

<sup>2</sup> *Journ. of Physiol.*, vol. xx., p. 223, 1896.

<sup>3</sup> *Comp. rend.*, vol. cxiii., p. 150, 1891.

<sup>4</sup> *Arch. de Physiol.*, vol. xxiv., p. 640, 1892.

<sup>5</sup> *Ibid.*, vol. xxviii., pp. 478 and 493, 1896.

tambour. Simultaneous blood-pressure tracings and plethysmographic tracings of other parts, spleen, kidney, etc., were also taken. They describe the vaso-constrictors as leaving the cord from the fifth thoracic downwards. The upper of these supply the upper part of the intestine, duodenum and jejunum, the lower part supplying the ileum and colon. Stimulation of the eleventh, twelfth, and thirteenth thoracic, and first and second lumbar white rami causes a constriction soon followed by a marked dilation of the vessel accompanied by a fall in blood pressure. These roots, therefore, contain the chief vaso-dilator fibres.

*Lower Part of Intestinal Canal.*—Fellner,<sup>1</sup> in working upon the innervation of the rectum, supports v. Basch's theory that where there is an organ with double muscular wall and double nerve supply, the one set of nerve fibres causes contraction of one muscular layer and inhibition of the second, whilst the other set of nerve fibres exerts the reverse effect. In accordance with this Fellner describes that in the dog stimulation of the nervus erigens causes contraction of the longitudinal and relaxation of the circular fibres of the rectum. Stimulation of the hypogastrics causes the reverse effects. Commenting upon this theory and Fellner's later experiments, Langley and Anderson write:<sup>2</sup> "We do not wish to assert that this theory applies in no case, but most certainly it is not one of general application. According to this theory the descending colon of the rabbit should receive from the lumbar nerves no inhibitory fibres for its longitudinal coat, and from the sacral nerves no motor fibres for its circular coat. In fact, when due care is taken inhibition of the longitudinal coat is produced by the lumbar nerves with undeniable distinctness; and the contraction of the circular coat produced by the sacral nerves is, at its best, one of the most striking visceral actions that can be brought about by stimulating any nerve in the body. At the same time we must state that our

<sup>1</sup> *Pflüger's Archiv*, vol. lvi., p. 542, 1893.

<sup>2</sup> *Journ. of Phys.*, vol. xviii., p. 104, 1895.



experiments do not disprove the statements of Fellner with regard to the innervation of the rectum in the dog, they only suggest that further observations are desirable."

We should note, however, that Gaskell<sup>1</sup> "entirely endorses" Fellner's conclusion. He obtained in the dog contraction of the longitudinal fibres of the rectum on stimulation of the nervus erigens, while, when the hypogastrics were stimulated, a distinct peristaltic contraction was observed. In the frog, too, he showed that fibres occurred in the seventh nerve, which, when stimulated, caused contraction of the circular muscles, and that the eighth and ninth nerves contained fibres stimulation of which caused contraction of the longitudinal muscles and pulling down of the rectum.

Langley<sup>2</sup> describes the effect of stimulation of the fibres of the upper region as inhibition of the descending colon and rectum, sometimes preceded by a brief contraction. The inhibition affects both longitudinal and circular fibres. The set of fibres from the sacral region produce a strong contraction of both sets of muscle.

With regard to the spinal roots, through which these two sets of fibres leave the cord, Bechterew and Mislowski<sup>3</sup> describe them as being the upper lumbar roots down to the sixth or seventh, and also the third sacral. The whole question has lately been closely gone into by Langley and Anderson.<sup>4</sup> In the rabbit the roots are the second to fifth lumbar inclusive, the third and fourth sacral, and, as a rule, either the second sacral or the first coccygeal. In the cat the second to fourth lumbar, the second and third sacral, and either the fifth lumbar or the first sacral. In the dog the origin of the lumbar fibres is slightly more anterior, and that of the sacral slightly more posterior than in the cat. The upper set of fibres in the rabbit causes, when stimulated, inhibition of the intestinal muscles (circular and longitudinal), sometimes a preliminary contraction which

<sup>1</sup> *Journ. of Phys.*, vol. vii., p. 26, 1885.

<sup>2</sup> *Ibid.*, vol. xii.; *Proc. Physiol. Soc.*, p. 23, 1890.

<sup>3</sup> *Arch. f. (Anat. u.) Phys.*, suppl., p. 243, 1889.

<sup>4</sup> *Journ. of Phys.*, vol. xviii., p. 67, 1895.

is then usually a circular contraction, only occasionally a longitudinal contraction. In the cat the same results are obtained, but are less marked because the intestines are more quiescent when exposed. The lower set causes contraction of both circular and longitudinal coats of rectum and descending colon and of the recto-coccygeal muscle. In the cat the same results were obtained, though contraction of the circular coat was not so constant, and when obtained was slight and took place slowly. With regard to their course, Langley and Anderson have shown by the degeneration method<sup>1</sup> and by the nicotine method<sup>2</sup> that the upper set of fibres run from the lumbar nerves to the inferior mesenteric ganglia direct, and there nearly all end in cells of that ganglion. Hence they run by branches from these ganglia—as colonic nerves—directly to the viscus. In the case of the second set of nerves, ganglion cells are present, and are placed near the viscus itself. Thus the upper set of nerve fibres are homologous with the related fibres contained in the splanchnics, the lower set with those in the vagi. With regard to the part played by the plexuses of Meissner and Auerbach, they were not able to obtain any special evidence of function. They conclude that the cells of these plexuses do not belong to the sympathetic system, but are of a different class.

*Vaso-motor* fibres for this part of the alimentary canal are found in both the upper and lower set of fibres. Stimulation of the upper set causes marked pallor of the descending colon and rectum, and of the mucous membrane of the anus. There are no vaso-dilators in this set. The cells on the course of the fibres are in the inferior mesenteric ganglion, or in the colonic nerves near their origin from that ganglion. The sacral set of fibres contain vaso-dilator fibres for the rectum, but they were not observed for the colon. The effect was not very marked in the cat, but rather better in the rabbit. These fibres have cells on their course placed near their termination in the viscus.

Steinach, for the frog finds nerves to the rectum in both

<sup>1</sup> *Journ. of Phys.*, vol. xvii., p. 177, 1894.

<sup>2</sup> *Ibid.*, vol. xix., p. 131, 1895.



anterior and posterior roots of the sixth and seventh spinal nerves. He obtains reflex contractions from stimulation of the posterior roots of one side after section of all the anterior roots on both sides, and of the posterior on the side stimulated.

*The anus.*—Sherrington,<sup>1</sup> when making observations on the fibres of the anterior roots forming the lumbo-sacral plexus, describes that when all the anterior roots of this region were cut the anus remained closed but less retracted than usual. On being opened by a sound it remained open after the sound was removed, but that on stimulation of some of these roots the anus being open, it was smartly closed by a contraction of the sphincter muscle. The roots which were effective in the cat were the eighth and ninth post-thoracic, sometimes the seventh. In *Macacus*, the root was the eighth, and either the seventh or ninth, though always to a less extent. When one root remained intact it did not remain patulous, and no asymmetry was produced by section of all three roots on one side. On excitation of a root when the anus was patulous a symmetrical contraction was obtained if the stimulus was strong, if weak sometimes an asymmetrical contraction was produced. Langley and Anderson<sup>2</sup> describe the upper set of fibres to contain in a rabbit inhibitory fibres for the internal sphincter, and obtained some evidence which, however, they did not consider very satisfactory, of motor fibres. In addition these fibres contained motor fibres for the non-striated muscles beneath the skin in the neighbourhood of the anus. These fibres chiefly innervated the half of the corresponding side. The origin from the cord was rather more restricted than for those fibres which innervated the colon and rectum. In the cat this set, on stimulation caused marked contraction of the internal sphincter. Stimulation of the sacral set of fibres in the rabbit caused dilatation of the internal sphincter and which was usually followed one or two seconds after cessation of the stimulus by a marked contraction. There are thus motor fibres for this muscle

<sup>1</sup> *Journ. of Phys.*, vol. xiii., p. 672, 1892.

<sup>2</sup> *Loc. cit.*

in these nerve roots. In the cat stimulation of these fibres may result in contraction or dilatation of the sphincter. The nerve cells on the course of the fibres of the upper set lie either in the superior mesenteric ganglia or in the ganglia in the hypogastric nerves. The cells on the lower set lie near the peripheral termination of the fibres.

*Spleen.*—Until the present year our knowledge of the innervation of this organ rested chiefly upon the work of Bulgak and Roy. Bulgak<sup>1</sup> relied upon direct observation of the spleen and showed that the nerves in the gastrosplenic omentum were of two kinds, afferent and efferent. Stimulation of the peripheral end of the latter caused a marked contraction of the spleen which was observed to pale in colour, its edges became more rounded and irregularities on its surface appeared. Stimulation of the peripheral end of the former nerves caused no effect, but when the central end was stimulated a marked reflex contraction was produced. He obtained big contractions by stimulating the semilunar ganglion or the peripheral end of the greater splanchnic on the left side. He observed no contraction on stimulating the peripheral end of the lesser splanchnic on the left side, or of either splanchnic on the right side. He traced these fibres still further backwards in their course, and localised them to the third to tenth thoracic anterior roots of the left side only, stating that no contraction was to be obtained by stimulating any of the roots above or below these or on the opposite side. He next examined the effect of the vagus upon the spleen and in opposition to previous observers found that stimulation of the nerve did not produce any contraction. The nerve was stimulated both above and below the point where it gave off its cardiac branches. Stimulation of the central end produces a large contraction, an effect which he suggests, is due to the interference with respiration, for he had previously observed that the splenic contractions were greatly increased by a venous condition of the blood. Roy<sup>2</sup> studied the rhythm and innervation of this organ by

<sup>1</sup> *Virchow Archiv*, lxix., p. 181, 1877.

<sup>2</sup> *Journ. of Physiol.*, vol. iii., p. 203, 1881.



employing his special plethysmographic method. He showed that the rhythmic contractions of the spleen might vary largely under different conditions. He obtained powerful contractions of the organ on stimulation of either splanchnic nerve and further differed from Bulgak in obtaining marked splenic contractions on stimulating the peripheral end of the cut vagus.

Quite recently a paper has appeared by Schäfer and Moore<sup>1</sup> in which this question is fully discussed. They show that the rhythm of the splenic contractions is quite independent of the nerves running to it though modified by them. Stimulation of either splanchnic in both dogs and cats produces a powerful contraction, better by the left nerve than by the right. In one case weak stimulation of the left splanchnic produced a dilation, whilst stronger and more frequent stimulation of the same nerves produced the ordinary contraction. In determining the outflow from the spinal cord they showed that the fibres in the splanchnic running to the spleen leave the cord in the anterior roots of both sides from the third to fourteenth post-cervical nerves inclusive. They are present in largest numbers in the sixth, seventh and eighth, and in fair numbers in the fifth, ninth and tenth. Of the similar roots of the opposite sides those on the left side produce a more marked effect than those on the right. In one case in a cat the same result was obtained. These results are all the more decisive in that they are able to obtain very sensitive records by employing a specially devised plethysmograph that is much simpler and more sensitive than Roy's instrument. They further investigated by the employment of the nicotine method as to whether there were any cells on the course of these fibres. Doses of five milligrammes, in succession, were administered by injection, and between each dose the nerves were tested in three parts of their course, in the anterior root, in the splanchnic, and at the hilum of the spleen. They thus show that there is a cell station which is easily paralysed by nicotine in the ganglia of the

<sup>1</sup> *Journ. of Physiol.*, vol. xx., p. 1, 1896.

sympathetic chain, and, moreover, that there is possibly a second series of cells, less readily paralysed by nicotine, between the splanchnics and the spleen, probably that is, in the semilunar ganglia. In connection with the position of the cells on these fibres, it should be noticed that these experimenters localise them to the lateral chain of ganglia, but that in the case of the nerves to the muscles of other viscera, intestines, etc., they have always been found to lie in the collateral ganglia. In regard, moreover, to the position of the cells on the vaso-motor fibres to the spleen, Schäfer and Moore's experiments point to a similar position for the majority of them. This view has been strongly questioned by Langley<sup>1</sup> who believes that, with the exception of a few aberrant fibres, all the vasco-constrictors of the splanchnics are in connection with cells of the solar plexus and of this plexus only.

#### NERVES TO THE GLANDULAR STRUCTURES OF THE RESPIRATORY AND ALIMENTARY TRACTS.

*The trachea and larynx.*—An increase in the rate of secretion of mucus from the glands in the mucous membrane of the trachea as a result of nerve stimulation has recently been proved by Kokin.<sup>2</sup> He experimented upon dogs and cats in which the trachea was laid open longitudinally in the mid-line by a galvano-cautery. The surface was then carefully dried and adherent mucus removed, and the time interval which elapsed before small, rounded drops of mucus appeared at the mouths of the ducts was noted. The same was repeated while various nerves were stimulated. Kokin thus finds secretory fibres in the vagus for these glands. In the dog the secretory fibres for the larynx and upper and middle portions of the trachea run in the superior laryngeal branch of the vagus. In the cat the inferior laryngeal contains fibres for the trachea and lower half of the larynx.

*To the submaxillary gland.*—In the cat Langley<sup>3</sup> has

<sup>1</sup> *Journ. of Physiol.*, vol. xx., p. 223, 1896.

<sup>2</sup> *Pflüger's Archiv*, vol., lxiii., p. 622, 1896.

<sup>3</sup> *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.



shown that the secretory fibres to the submaxillary gland leave the cord mainly in the second and third thoracic nerve roots; once only has he obtained secretion from the first, fourth or fifth thoracic. In the dog the origin is slightly different. In this animal the first and second thoracic always contain secretory fibres, the third, fourth and fifth only containing some in one out of three cases.

These fibres end in cells of the superior cervical ganglion.<sup>1</sup> Thence passing through the grey rami of the ganglion the fibres reach the gland *via* the sympathetics on the carotid and facial arteries. There are no further cells on these fibres. The position of the cells on the course of these sympathetic secretory fibres has also been located to the superior cervical ganglion by the aid of the method of degeneration. This has been effected by Langley<sup>2</sup> and by Bradford<sup>3</sup> for the cat.

The chorda tympani fibres to the gland have also been shown to possess nerve cells on their course. In the dog these<sup>4</sup> are found on the course of the chorda tympani just at its entrance into the hilum of the submaxillary gland or shortly before this. In the cat many more are found in the nerve before its entrance into the gland. The præ-ganglionic fibres therefore are from the origin of the seventh cranial nerve along the chorda to its termination at the gland; and the post-ganglionic from this point to their distribution in the gland substance. Langley also shows that the cells in the submaxillary ganglion and in the triangle lying between the duct, the lingual nerve and the chorda, are in connection with fibres to the sublingual gland not to the submaxillary.

By the injection of nicotine the sympathetic cells are paralysed before the chorda cells, in the cat, and recover later. In the dog they however recover quickly.

The *vaso-constrictor* fibres to the submaxillary gland

<sup>1</sup> Langley and Dickinson, *Proc. Roy. Soc.*, vol. xlvi., p. 423, 1889, and Langley, *Journ. Physiol.*, vol. xi., p. 123, 1890.

<sup>2</sup> *Journ. of Physiol.*, vol. vi., p. 87, 1885.

<sup>3</sup> *Ibid.*, vol. ix., p. 302, 1888.

<sup>4</sup> *Loc. cit.*

arise from the thoracic cord in the same roots as the secretory fibres and run up the cervical sympathetic to the superior cervical ganglion where they terminate. From the nerve cells influenced by them the post-ganglionic fibres run along the carotid and facial nerve-plexuses and so reach the gland. There are no other nerve cells on the course of the fibres running up the cervical sympathetic other than those in the superior cervical ganglion.<sup>1</sup>

With regard to the *vaso-dilators* to the submaxillary and sublingual glands passing along the chorda-tympani, Langley<sup>2</sup> has shown that those for the submaxillary gland are in connection with cells in the chorda-tympani at or near its entrance into the hilum of the gland; those for the sublingual gland have their cells in the submaxillary ganglion, or in the triangle formed by the duct, the lingual nerve and the chorda tympani.

For an account of what is known of the secretory fibres to the stomach and pancreas, I would refer to the recent number of "SCIENCE PROGRESS"<sup>3</sup> containing Starling's paper, "Pawlow's Researches on the Physiology of Secretion".

*To the liver.*—Bernard observed that an increase in the amount of glucose in the blood, and a consequent glycosuria could be brought about by stimulation of the central end of the divided vagus, or better by alternate stimulation of the central and peripheral ends. He further noted that on the death of an animal consequent on section of both vagi in the neck there was a complete disappearance of sugar from the blood and from the tissues generally.

E. Cavazzani<sup>4</sup> found changes in the liver cells following stimulation of the coeliac plexus in dogs and rabbits which were comparable to changes occurring in glands on stimulation of their nerves. On comparing the appearances of the cells in a piece of the liver which had been stimulated

<sup>1</sup> See Langley, *Journ. of Physiol.*, vol. xi., p. 153, 1890, and Langley, *Journ. of Physiol.*, vol. vi., p. 87, 1885.

<sup>2</sup> *Journ. of Physiol.*, vol. xi., p. 123, 1890.

<sup>3</sup> Feb., 1896, vol. iv., p. 491.

<sup>4</sup> *Pflüger's Arch.*, vol. lvii., p. 81.



in this way, with cells from a second portion of the same liver which had been at rest, he observed histological differences exactly comparable to the appearances of liver cells taken from fasting and from well-fed animals.

Butte<sup>1</sup> repeated Bernard's experiments on section of the two vagi in the neck. The dogs died from twenty to forty-six hours after the section, and in no case was any glycogen found in the liver. In other experiments he<sup>2</sup> also showed, in confirmation of Bernard's original observation, that stimulation of the peripheral end of the divided vagus causes a diminution of the amount of glycogen in the liver, and an increase in the amount of glucose in the blood.

Cavazzani<sup>3</sup> shows that this same result may be obtained by stimulation of the cœliac plexus in dogs, and that the quantity of glycogen disappearing corresponds to the quantity of glucose formed.

Levene<sup>4</sup> confirms this production of glucose on vagus stimulation, but still found glycogen in the liver, and sugar in the blood, three days after section of both vagi.

Morat and Dufourt<sup>5</sup> show that the sugar formation is due to nervous action not to alterations in the circulation of the liver. In a later paper<sup>6</sup> they show that stimulation of the splanchnics, by induction shocks after division, or by asphyxia, leads to a disappearance of glycogen and a corresponding increase in the amount of glucose. This is obtained both while the circulation is intact or when it is stopped by ligature of the aorta and portal vein.

*Vascular nerves to the liver.*—By simultaneous records of the aortic blood pressure, and that in the portal vein, Bayliss and Starling<sup>7</sup> have mapped out the spinal origin of the constrictor fibres to the portal vein. These leave the cord in the third to eleventh thoracic roots inclusive, only

<sup>1</sup> *Comp. Rend. Soc. de Biol.*, vol. xlv., p. 734, 1894.

<sup>2</sup> *Ibid.*, p. 166, 1894.

<sup>3</sup> *Ann. di chimica e farmacologia*, Bologna, 1894, abstracted in Maly's *Jahres-Bericht*, vol. xxiv., p. 391, 1895.

<sup>4</sup> *Centr. f. Physiol.*, vol. viii., p. 337, 1894.

<sup>5</sup> *Compt. Rend.*, vol. cxviii., p. 659.

<sup>6</sup> *Arch. de Physiol.*, vol. xxvi., p. 371, 1894.

<sup>7</sup> *Journ. of Physiol.*, vol. xvii., p. 120, 1894.

a few being found in the third and fourth, and tenth and eleventh anterior thoracic roots. The nerves to the hepatic artery have been investigated by Cavazzani and Manca.<sup>1</sup> Their method was to establish an artificial circulation and then determine the amount of outflow under different circumstances. They find vaso-dilators in both the splanchnic and vagus, and constrictors in the splanchnic. Asphyxia causes a dilation which is not produced when the vagi are cut. Stimulation of the coeliac plexus low down causes better dilatation than stimulation of the vagus.

*Innervation of the Thoracic duct.*—By determinations of the rate of outflow of a fluid at constant pressure passing through the Thoracic duct, Camus and Gley<sup>2</sup> have obtained evidence of the presence of nerves, causing both dilation and constriction of the duct, in the sympathetic chain under the first thoracic ganglion. As a rule the dilator effect is produced.

#### NERVES TO THE GENITO-URINARY SYSTEM.

*To the kidney.*—Bradford<sup>3</sup> has determined the origin of the vascular nerves to the kidney by observations of the changes in its volume on excitation of the various anterior roots. He finds that the vaso-constrictors are mainly contained in the eleventh, twelfth, and thirteenth thoracic nerves, to a less extent in the seventh, eighth, ninth, and tenth thoracic, and sometimes in the sixth thoracic and first and second lumbar nerves. He determined the presence of vaso-dilator nerves by stimulating with induced shocks, repeated only once per second, or once in two seconds. By this method he was able to show the existence of dilator fibres to the kidney in the eleventh, twelfth, and thirteenth thoracic nerves.

Langley and Dickinson<sup>4</sup> have shown that the nerve cells on the course of the constrictor fibres are situated in the coeliac, mesenteric, or renal ganglia, and that the cells

<sup>1</sup> *Arch. Ital. de Biol.*, vol. xxiv., pp. 33 and 295, 1895.

<sup>2</sup> *Arch. de Physiol.*, vol. vii., pp. 301, 328, 1895.

<sup>3</sup> *Journ. Physiol.*, vol. x., p. 358, 1889.

<sup>4</sup> *Proc. Roy. Soc.*, vol. xlv., p. 423, 1889.



on the course of the dilator fibres are placed in the solar plexus and renal ganglia.

*The bladder.*—When considering the innervation of this viscus we have again to note that we are dealing with one which, as commonly described, possesses a double muscular wall and a double nerve supply, an upper one from the lumbar nerves and a lower from the sacral *viâ* the nervi erigentes. With regard to the question of the reversed function of the two sets of fibres on the two muscular coats (v. Basch's theory), we have evidence leading to a similar conclusion as in the case of the colon. Thus Griffiths<sup>1</sup> brings evidence of an anatomical nature that in reality we have to deal with a viscus possessing a single muscular wall. Zeissl,<sup>2</sup> on the contrary, argues from his experiments that the sacral set cause, when stimulated, contraction of the detrusor urinæ and inhibition of the sphincter, and that the hypogastrics cause contraction of the sphincter and inhibition of the detrusor urinæ, though the evidence of this last action he does not consider very satisfactory. Langley and Anderson, however, take the opposite view, and consider that the interpretation which Zeissl has placed upon his results is not the correct one. Their experiments show that stimulation, of both the hypogastric and pelvic (nervus erigens) nerves, causes contraction of both longitudinally and circularly arranged muscle bundles.

In reviewing the experiments of those who have been working in recent years upon the origin and course of fibres which innervate the bladder, we may first notice those of Navrocki and Skabitschewski,<sup>3</sup> who worked upon curarised dogs, and observed the movements of the bladder directly by the naked eye. This method they chose as the only one giving certainly reliable results, for they found that the introduction of a catheter, or tying in a tube into the apex of the bladder, led to irregular contractions, which tended to make results by such methods unreliable. The

<sup>1</sup> *Journ. of Anat. and Phys.*, vol. xxv., p. 535, 1891.

<sup>2</sup> *Pflüger's Archiv*, vol. liii., p. 560, 1893.

<sup>3</sup> *Ibid.*, vol. xlviii., p. 335, 1891.

upper set of fibres they traced passing through the fourth and fifth anterior lumbar roots, to the sympathetic chain by white rami communicantes, thence by the mesenteric nerves to the inferior mesenteric ganglion, then along the hypogastrics to the hypogastric plexus, and so by the vesical plexus to the bladder. The lower set left the cord in the second and third sacral nerves, and reached the hypogastric plexus by the pelvic nerve, and so on to the bladder. Stimulation of either of these two sets caused marked contraction of the bladder.

Sherrington<sup>1</sup> recorded the movements of the bladder, consequent upon stimulation of the anterior roots of the lumbar and sacral nerves, by means of a water manometer connected to the interior of the bladder by a catheter. In the cat he describes the effective roots, as being the third and four lumbar, together with either the second or fifth, or occasionally both. Of the lower set the second sacral was the chief root, and the first and third usually contained fibres having this function. In *Macacus Rhesus* he found the third and fourth lumbar with either the second or fifth, and the second sacral with the first and third to less extent. The lower set always produced the more powerful contraction which was unilateral when a nerve root of one side was stimulated.

Griffiths<sup>2</sup> found that stimulation of the pelvic nerve produced a more powerful contraction than stimulation of the hypogastric, but that both of them produced contraction throughout the entire thickness of the muscular coat. Stimulation of the nerves on one side produced unilateral contraction of the bladder. Langley and Anderson<sup>3</sup> found that stimulation of either set of nerves caused contraction of the whole muscular coat, but did not get a unilateral contraction on stimulating the nerves of one side, though the contraction on the same side was much better marked than on the opposite side. The upper set of fibres left the cord in either the second and third or third and fourth, or fourth

<sup>1</sup> *Journ. of Phys.*, vol. xiii., p. 677, 1892.

<sup>2</sup> *Journ. of Anat. and Phys.*, vol. xxix., pp. 61 and 254, 1895.

<sup>3</sup> *Journ. of Phys.*, vol. xix., p. 71, 1895.



lumbar roots in the dog ; in the cat chiefly by the fourth occasionally by the third and fifth, and in the rabbit by the fourth and fifth, together with either the third or second lumbar.

These fibres pass, by the mesenteric nerves, from the sympathetic chain to the inferior mesenteric ganglion, thence by the hypogastrics to the bladder. Nerve cells in their course can be shown by the nicotine method. They are either situated in the inferior mesenteric ganglion or along the course of the hypogastrics. Stimulation of this set causes a much weaker contraction than stimulation of the sacral set, a contraction not sufficiently powerful to cause micturition. The lower set of fibres occur, in the rabbit, in the third and fourth sacral with a few in the second, or in the second and third sacral with a few in the fourth ; in the cat, in the second and third sacral, occasionally in the first, and in the dog, in the second and third sacral with sometimes a few in the first coccygeal. Stimulation of these fibres causes micturition. They reach the bladder *via* the pelvic nerves and hypogastric plexus. Their course is broken by nerve cells which occur scattered along the course of the fibres usually near the viscus itself, *e.g.*, in its lateral ligament. Inhibitory fibres were looked for but without any positive result ; they consider that if any be present they are only few in number. Recently Courtade and Guyon<sup>1</sup> have published results of experiments upon this subject which, however, only confirm some of our previous knowledge. They are apparently unacquainted with the papers of Sherrington, Griffiths, and Langley and Anderson.

In the frog Gaskell<sup>2</sup> found two sets of fibres corresponding to those in mammals. The lower set occur in the eighth and ninth spinal nerve roots, and stimulation of them caused marked contraction of the longitudinal coat. The upper set are represented by fibres in the seventh nerve, which he describes as causing contraction of the

<sup>1</sup> *Arch. de Phys.*, vol. xxviii., p. 622, 1896.

<sup>2</sup> *Journ of Phys.*, vol. vii., p. 26, 1886.

circular fibres. Bernheim<sup>1</sup> in frogs and salamanders found fibres for the bladder in the eighth and ninth nerves, sometimes in the tenth as well. Steinach<sup>2</sup> found nerves for the bladder of the frog not only in the anterior roots of the seventh, eighth and ninth nerves, but also in the posterior roots of those same nerves. He confirms their presence in these posterior roots, by obtaining a reflex contraction of the bladder after all the anterior roots of these nerves had been cut on both sides, and the posterior as well on one side.

Very few, if any, *vaso-motor* nerves are contained in the lumbar set of nerves<sup>3</sup> to the bladder, nor were Langley and Anderson able to show their presence in the sacral set of fibres.<sup>4</sup>

*External genital organs.*—Langley and Anderson<sup>5</sup> have examined the lumbar and sacral nerves with especial reference to these organs.

Here again the nerves arise in two sets, an upper and a lower. The upper set of nerves in the male cause when stimulated a powerful contraction of the retractor muscle of the penis, contraction of the intrinsic muscles of the penis, of the unstriated muscles of the genital skin, and of the dartos and cremaster muscles. Stimulation of the lower set of fibres causes very marked inhibition of the retractor muscle, of the non-striated muscles of the penis and of the skin, with contraction of the striated erector muscles, *viz.*, the recto-cavernosus, the ischio cavernosus, the bulbo-cavernosus, Houston's muscle and the striated muscle of the urethra. In the female, the upper set cause contraction of the vulva and of the skin muscles, with slight retraction of the clitoris; the effects sometimes are very slight especially in the cat and dog. The lower set cause dilatation of the vulva, relaxation of the skin muscles around the vulva and contraction of the muscles which correspond to the

<sup>1</sup> *Arch. f. (Anat. u.) Phys.*, suppl., p. 11, 1892.

<sup>2</sup> *Pflüger's Archiv*, vol. lx., p. 593, 1895.

<sup>3</sup> *Journ. of Phys.*, vol. xix., p. 75, 1895.

<sup>4</sup> *Loc. cit.*, p. 79.

<sup>5</sup> *Journ. of Physiol.*, vol. xix., p. 85, 1895.



striated genital muscles of the male. The upper set of fibres leave the cord in the cat either in the third and fourth lumbar with a few in the fifth, or in the fourth and fifth with a few in the third, occasionally there are some in the second. In the dog their origin is a little more anterior, for there are never any in the fifth. In the rabbit they pass out in the third, fourth and fifth. Sherrington<sup>1</sup> observed contraction of the cremaster muscle on stimulation of the second and third anterior roots of lumbar nerves in rhesus, in one case the fourth lumbar was found to be effective instead of the second.

The posterior set, in the cat, are found in the first and second, occasionally in the third sacral ; in the rabbit in the second, third and fourth sacral anterior roots. Sherrington<sup>2</sup> observed a sharp closure of the vaginal orifice on stimulation of the second and third sacral nerves in the cat, and in rhesus. As a rule the third nerve was more effective than the second, and the contraction was bilateral.

The course of the upper set of fibres is by the white rami to the sympathetic chain, whence they may travel by two paths, either to the pudic nerve or *vià* the pelvic plexus. The great majority of the fibres leave the chain by the sacral grey rami to the sacral nerves, and reach their destination by the dorsal nerves of the penis or clitoris, the genito-anal and the scrotal nerves. A certain number of this set—but relatively few—run by the hypogastric nerves. The visceroinhibitory fibres in the sacral nerves all pass into the pelvic visceral branches of those nerves. The fibres to the striated erector muscles run direct through the perineal nerve, genito-anal nerves and the nervus dorsalis.

The upper set of fibres have nerve cells upon them which for those which travel by the sacral grey rami are placed in the sacral ganglia, for those which travel by the hypogastric are placed in the hypogastrics or a little nearer their peripheral ends.

Of the lower set of fibres those which run to striated muscles resemble ordinary motor nerves, and have no nerve

<sup>1</sup> *Journ. of Physiol.*, vol. xiii., p. 683, 1892.

<sup>2</sup> *Ibid.*, p. 675, 1892.

cells on their course. The inhibitory fibres passing through the nervi erigentes have cells on their course, placed close to the urethra or in the organs themselves.

*Vaso-motor nerves to these parts.*—Stimulation of the lumbar set of fibres causes strong contraction of the arteries to the penis or clitoris, and a slighter contraction of the vessels to the surrounding genital skin and scrotum. The origin of these fibres from the cord is in the main similar to that given above, though in the cat the thirteenth thoracic and first lumbar were also effective.

The nerve cells on the course of these fibres are placed similarly to those on the other visceral fibres running from the lumbar set. They did not find any satisfactory evidence of the presence of vaso-dilators in these fibres. The lower set of fibres contain many vaso-dilators but no vaso-constrictors. Gaskell<sup>1</sup> found vaso-dilators to the penis in the second and third sacral anterior roots in the rabbit. They were never present in any posterior roots. Sherrington<sup>2</sup> obtained the same result in rhesus and in the cat. Francois Franck<sup>3</sup> investigated the vascular nerves to the penis by a plethysmographic method, and recorded at the same time the changes in arterial and venous pressure in the organ. He finds that the mesenteric nerves to the inferior mesenteric ganglia from the sympathetic chain contain many vaso-dilators, and also vaso-constrictors though in fewer numbers. The pelvic nerves contain many vaso-dilators. His experiments were carried out upon dogs which were curarised in order to prevent complications by other muscular influences.

*Internal generative organs.*—Our knowledge of the innervation and course of the fibres to the internal generative organs also largely depends upon the researches of Langley and Anderson.<sup>4</sup> They find that for these pelvic viscera there is only one set of nerves, which come from the lumbar roots. These cause very strong contraction of the

<sup>1</sup> *Journ. of Physiol.*, vol. viii., 1887. *Proc P. S.*, p. 4.

<sup>2</sup> *Ibid.*, vol. xiii., p. 686, 1892.

<sup>3</sup> *Arch. de Physiol.*, vol. xxvii., pp. 122 and 138, 1895.

<sup>4</sup> *Journ. of Phys.*, vol. xix., p. 122, 1895.



muscular coat of the uterus and vagina, or of the vas deferens and vesiculæ seminalis (uterus masculinus) in the rabbit. In the cat the same contraction results though not to so marked an extent. The contraction involves both muscular coats. In the dog the contraction of the vas is not well marked, the longitudinal contraction which is so marked a feature in the rabbit is almost absent; this is to be associated with the fact that in the dog the longitudinal muscular coat is poorly developed. Unilateral stimulation of the nerves causes unilateral contraction of the vas, but bilateral contraction of the vesicula seminalis—a contraction which is strong enough to eject semen. These fibres occur chiefly, in the rabbit, in the fourth lumbar and to a less extent in the third and fifth anterior lumbar roots. In the cat they are found chiefly in the third and fourth with a few in the second lumbar.

Sherrington<sup>1</sup> observed contraction of the vas to occur as the result of stimulation of the second and third lumbar anterior roots in rhesus; in the cat from the third and fourth lumbar. The contraction had a long latent period and was of a peristaltic nature, involving both muscular coats. In the female contraction of the fibres in the round ligament followed stimulation of the second and third lumbar, or sometimes in the fourth lumbar in rhesus, and of the third and fourth lumbar in the cat.<sup>2</sup> In rhesus this muscle is striated. Langley and Anderson also note contraction of the unstriated fibres in the meso-metrium on stimulating the lumbar nerves.

The fibres leave the corresponding nerves as white rami and pass to the sympathetic chain, whence, as a rule, they pass to the inferior mesenteric ganglion, and by the hypogastric nerves to the pelvic plexus and their final distribution. The nerve cells on the course of these fibres are situated either in the inferior mesenteric ganglion or in ganglion cells placed further on their course in the hypogastric nerves. This has been proved by the nicotine method, and also by examination of the fibres after de-

<sup>1</sup> *Journ. of Phys.*, vol. xiii., p. 685, 1892.

<sup>2</sup> *Loc. cit.*, p. 684.

generation of the preganglionic segment has been brought about by section of the lumbar nerves.<sup>1</sup>

With regard to the question of the presence of a second set of fibres in the sacral nerves, Langley and Anderson are not able to confirm the observations of previous workers that such exist. They obtained negative results on stimulating the sacral nerves, and were, moreover, led to the same conclusion, as a result of the tracing of degenerated fibres following section of the sacral nerves.<sup>2</sup>

The *vaso-motor* nerves to these parts take the same course as the fibres to the muscular walls. Stimulation of the efficient nerves causes, in addition to the previously mentioned effects, marked pallor of uterus, vagina, and vestibule in the female, and of the vas and seminal vesicles in the male. They have the same course and similar nerve-stations as the visceromotor fibres.

#### NERVES TO SWEAT GLANDS.

Langley,<sup>3</sup> working upon the sweat glands in the pads of the cat's feet, describes the origin of the fibres for the fore feet to lie in the fourth to tenth thoracic inclusive. They mainly run in the sixth, seventh, and eighth thoracic anterior roots, to a less extent in the fifth and ninth, still less in the fourth, and only occasionally in the tenth thoracic. All these fibres run upwards, and end in cells in the ganglion stellatum. From this they issue in the grey rami to the nerves of the brachial plexus, and thence to their distribution. The combined sixth and seventh white rami supply chiefly the inner part of the foot.

For the hind foot they leave the cord in the first and second lumbar, to a rather less extent in the thirteenth thoracic, and still fewer in the twelfth thoracic and third lumbar; and when the lumbo-sacral plexus is posterior in the fourth lumbar. None of these fibres leave the sympathetic cord above the sixth lumbar ganglion or below

<sup>1</sup> *Journ. of Phys.*, vol. xviii., p. 177, 1894; vol. xix., p. 372, 1896.

<sup>2</sup> *Ibid.*, vol. xix., p. 372, 1896.

<sup>3</sup> *Ibid.*, vol. xii., p. 347, 1891; vol. xvii., p. 296, 1894-5. A full account of the earlier literature is given in this paper.



the second sacral. They pass out from the sixth and seventh lumbar and first and second sacral ganglia, being connected with cells in those ganglia. As a rule the fibres leaving in a grey ramus of a ganglion are connected to the cells in that ganglion, but in a few cases the cells are situated in the ganglion above. In a few cases none are found in the second sacral, and then nearly always the lumbo-sacral plexus is found to be of the anterior type. Those fibres given by the sixth ganglion are chiefly supplied to the inside of the foot, and those from the second sacral to the outside. Stimulation of the grey ramus from the first sacral causes a marked secretion on the outer side, and a less prominent secretion on the inner side. Stimulation of the seventh lumbar gives a less regular result, commonly there is a secretion all over the foot, sometimes more marked on the inner side.

There are no secretory fibres running directly to the glands from the cord through the sciatic roots.

#### NERVES TO THE EYEBALL.

As recorded by Bernard,<sup>1</sup> it was Biffè who first showed that stimulation of the upper end of the cut cervical sympathetic caused dilation of the pupil. Petit,<sup>2</sup> from a study of the course of the fibres from the fifth and sixth thoracic nerves into the cervical sympathetic, as given by Willis and Vieussens, came to the conclusion, in opposition to them, that the fibres were running from the cord to the neck, not in the reverse direction. To test this, he cut the cervical sympathetic, and discovered that the pupil was permanently constricted.

Budge and Waller<sup>3</sup> also found that stimulation of the peripheral end of the cut cervical sympathetic caused dilation of the pupil, an effect not to be obtained on stimulation of the nerve one month after its section. By stimulation of the spinal cord, they obtained this dilatation

<sup>1</sup> *Journ. de Physiol.* (Brown-Séquard), vol. v., p. 383, 1862.

<sup>2</sup> *Histoire de l'Académie des Sciences*, 1727.

<sup>3</sup> *Comp. Rend.*, vol. xxxiii., pp. 370, 418, 1851.

effect best, on stimulating at the second and third thoracic segments, and came to the conclusion that these two nerves are those carrying the fibres. They further traced the fibres as passing through the Gasserian ganglion into the ophthalmic branch of the fifth cranial nerve. Bernard<sup>1</sup> observed in addition a drawing back of the eyeball and a fall of the eyelids after section of the nerve. By cutting both the first and second thoracic anterior roots he obtained the same result. Langley and Dickinson<sup>2</sup> showed, by the nicotine method, that there were nerve cells on the course of these fibres, which are situated in the superior cervical ganglion. By stimulation of the anterior roots, Langley<sup>3</sup> finds that in the dog and cat the fibres leave by the first and second thoracic nerves, occasionally by the third, though as a rule these latter only run to the nictitating membrane and eyelids. In the rabbit the second and third thoracic are the chief nerves, the first exerting but slight action. There are no other nerve cells on their course other than those in the superior cervical ganglion.

*Nerves to the splincter iridis and ciliary muscle.*—Langley and Anderson<sup>4</sup> have shown that at any rate the main number of cells in the ciliary ganglion, are on the course of the fibres to these muscles. After the injection of ten milligrams of nicotine, stimulation of the third nerve produces no effect, though stimulation of the short ciliary nerves still produces the usual result.

On a review of the whole of the facts of the general efferent innervation of the structures developed from the splanchnic mesoblast, we find that we may draw certain generalisations.

In all thoroughly investigated cases, the nerve chain uniting the central nervous system with the peripheral organ consists of two links, each consisting of a nerve cell and its fibre. The upper one, with its cell placed

<sup>1</sup> *Comp. Rend., Soc. de Biol.*, vol. iv., pp. 155, 168, 1852; and *Comp. Rend.*, vol. xxxvi., p. 375.

<sup>2</sup> *Proc. Roy. Soc.*, vol. xlvii., p. 379, 1889-90.

<sup>3</sup> *Phil. Trans.*, vol. clxxxiii., p. 85, 1892.

<sup>4</sup> *Journ. of Physiol.*, vol. xiii., p. 460, 1892.



in the central grey matter, terminates dendritically at the position of the second nerve cell. The second cell is found situated in various positions, either in the lateral chain of ganglia, *i.e.*, those having a white ramus running to them, or in the collateral ganglia such as the superior cervical ganglion, or the mesenteric ganglia, or finally, in peripheral ganglia placed in or very near the organs themselves, *e.g.*, in the heart, the internal generative organs, etc. In his latest paper, Langley<sup>1</sup> gives, as the conclusion he has drawn from his many experiments, that "each visceral nerve fibre has one nerve cell on its course and one only. More accurately, that a visceral nerve impulse on its way from the central nervous system to the periphery traverses one nerve cell and one only." He considers that each fibre which leaves the central nervous system divides, and that each division is connected with a nerve cell. As a rule all the divisions terminate in the same ganglion, but in some cases there is evidence to show that one or more of the collateral divisions may terminate in a second ganglion, or along a nerve strand, proximally or distally to the termination of the major number of the divisions. Further, that where there are several præ-ganglionic fibres running to the same or to analogous parts, they nearly all terminate in the same ganglion, though here again exceptions may occur, some few fibres terminating with a slightly shorter or longer course.

In many cases the post-ganglionic fibre is non-medullated, but this is by no means a general rule, for Langley<sup>2</sup> has shown that many finely medullated fibres occur in grey rami and elsewhere which are neurons from cells in the various ganglia.

A point of considerable interest is with regard to the part played by the nerve cell which is interpolated upon the course of the fibres uniting the viscera to the centre. Reflexes may be obtained from some of these ganglia, but Langley and Anderson have shown that these reflexes are

<sup>1</sup> *Journ. of Physiol.*, vol. xx., p. 223, 1896.

<sup>2</sup> *Ibid.*, p. 55, 1896.

not true reflexes, as they occur in the grey matter of the cord, but are probably due to the stimulus running up an efferent fibre and down a collateral of that same fibre and so bringing about the muscular contraction. Another view of the part played by the cells is that through them the fibre loses its medulla and becomes non-medullated; but this we have seen is not general. There is a final suggestion that a few nerve fibres run to these cells, and that many more fibres run from them. That, in a way then, there is a multiplication of fibres as they travel through the ganglion, a point which will require only a few fibres to run from the cord and yet readily allow of a wide peripheral distribution. This is of course an obvious advantage where a large peripheral area is always required to work as a whole and in the same sense.

The general arrangement of the nerve cells anatomically as contrasted physiologically also shows some uniformity, and allows us to draw conclusions with respect to the morphological inter-relationships of the various ganglia. Thus, in the lateral chain of ganglia we find the cells on the course of the pilo-motor nerves, splenic nerves, and some vaso-constrictors (to surface of trunk). In the collateral chain are found the cells of many vaso-constrictors, of the nerves to sweat glands, salivary glands, of the inhibitory fibres to the alimentary canal, and of the cardiac accelerators, whilst in the terminal ganglia are placed among others the cells on the cardio-inhibitors, on the motor fibres to the lower part of the intestine and bladder, on the inhibitory fibres to the external genital organs, etc.

It is also of value to compare the different positions of the cells for analogous fibres to different organs. Treating the vaso-constrictors in this way we see that the cells are placed for the trunk in the corresponding lateral ganglia; for the upper limb in the ganglion stellatum; for the lower limb in the sixth and seventh lumbar, and first and second sacral; for the tail in the coccygeal ganglia; for the stomach in the cœliac ganglion; for the small intestine in the superior mesenteric; for the large intestine and rectum in the inferior mesenteric; for the external genitals in the



sacral ganglia ; for the head in the superior cervical ganglion ; for the submaxillary and sublingual glands in the superior cervical ganglion, etc.

The cells on the vaso-dilator fibres are placed in the superior cervical ganglion for the gums and lips, in the hilum of the gland for the submaxillary, near the viscus for the rectum or external genitals, etc.

The cells for the motor fibres of the upper part of the alimentary canal are in the ganglion trunci vagi, for the lower part, on the course of the fibres near the viscus. The cells on the inhibitory fibres of the upper part of the alimentary canal are in the cœliac or superior mesenteric ganglia, for the lower part in the inferior mesenteric ganglia or along the course of the colonic nerves or hypogastrics.

T. GREGOR BRODIE.

## NOTES ON PARASITES.

### I.

**A**MONGST the many doubtful points which have exercised the minds of those Zoologists who work at the parasitic worms, none has caused a greater divergence of opinion than the question of the existence or non-existence of an external epithelium. Since Rindfleisch and shortly afterwards A. Schneider, some thirty years ago, denied that such a layer existed, hardly any two writers have agreed as to the nature of the skin of Cestodes and Trematodes. All, however, have recognised the existence of a cuticle, but as to its nature there were almost as many opinions as there were writers. Rindfleisch and A. Schneider regarded it as the basement membrane of a lost epithelium, and this view was adopted by Leuckart and consequently gained a wide acceptance; other writers, however, held that the cuticle was itself the external epithelium which had become much modified and had lost all trace of cells and nuclei.

The recent researches of Professor Blochmann<sup>1</sup> of Rostock have done much to clear up this and many other doubtful points in the histology of the Cestodes and Trematodes. These researches have been largely facilitated by the employment of Golgi's method of staining and by the use of the Iron-hæmatoxylin staining fluid: they were chiefly carried out on *Ligula monogramma*, though twelve other species of Tape-worm and many Trematodes were also investigated.

Blochmann begins his paper by pointing out that if there is no external epithelium we must invent a new name for the cuticle, since it is of the essence of a cuticle that it should be formed from the free ends of epithelial cells; secondly, that external unicellular glands such as are common in Trematodes and also occur in Cestodes, though less frequently, are as a rule produced by the modification of

<sup>1</sup> *Die Epithelfrage bei Cestoden und Trematoden*, Hamburg, 1896.



some of the cells of an epithelial layer ; and finally that absorption, which presumably takes place all over the body of Tape-worm, is usually in other animals effected by an epithelium. All these statements make it probable that such an epithelium exists, and Blochmann's preparations demonstrate its existence in the parasites in question, although in a somewhat modified form.

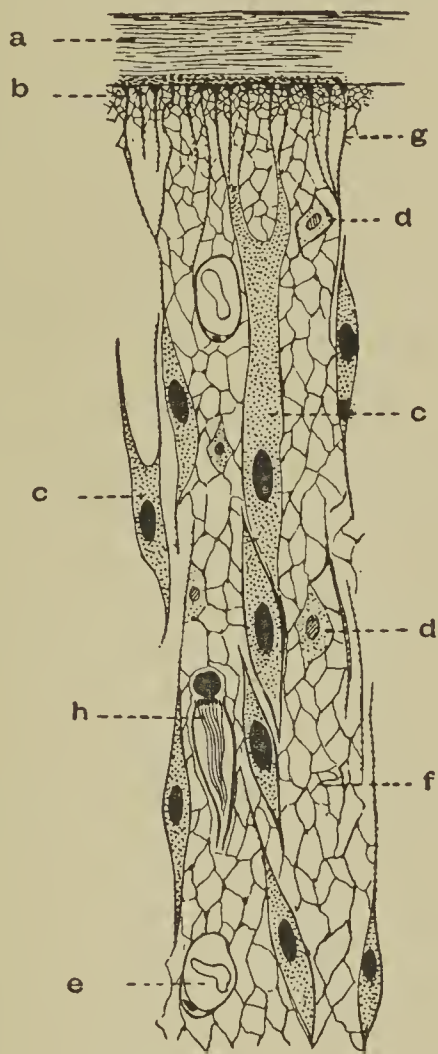


FIG. 1.—Transverse section through the outer part of the body wall of *Ligula monogramma*  $\times 800$ . After Blochmann. The muscles have been in all cases omitted.

- a.* Cuticle.
- b.* Basement-membrane composed of close network of fibrils.
- c.* Epithelial cells.
- d.* Branching cells of parenchyma.
- e.* Cell of parenchyma containing a calcareous body.
- f.* Parenchymatous network.
- g.* Processes of epithelial cell terminative in swollen ends in the cuticle.
- h.* Flame cell of excretory system.

The body of a Cestode such as *Ligula* consists of a parenchyma or ground-substance (Fig. I. *f*) of the nature of connective tissue in which lie embedded the various organs, and which is traversed in various directions by muscular and nervous strands. According to Blochmann the external epithelium has to some extent sunk into this

parenchyma so that we do not find a sheet of contiguous epithelial cells on the inner side of the cuticle, but, instead, a thin layer of the parenchyma which in common with other authors he calls the basement membrane (Fig. I. *b*). Situated below this, though at slightly different levels, are a number of spindle-shaped cells with well-marked nuclei, these represent the external epithelial layer of other animals (Fig. I. *c*). Although the bodies of these cells are separated from the cuticle by the basement-membrane mentioned above, they have not lost their original connection with the external surface, but send up fine processes, often several from one cell, which pass through the basement membrane and terminate in the cuticle (Fig. I. *g*). The lateral separation of epithelial cells from one another which is here seen to be due to the intrusion of the parenchyma is paralleled in the case of the leech, where the connective tissue, often carrying with it minute blood-vessels, penetrates between the cells of the ectoderm. This feature is particularly well marked in preparations made from the body wall of a leech which has recently enjoyed a full meal.

The parenchyma of Cestodes, like other connective tissues, consists of cells and a ground substance. The cells are very richly branched (Fig. I. *d*), their finer ramifications stretching through the body in all directions, surrounding all the organs and often accompanying for some distance the muscle fibres. Their processes anastomose with those of other cells such as the epithelial cells and thus the parenchyma cells are in a position to play a large part in the nutrition of the parasite. They secrete the ground substance which they throw off in the form of fine membranes and strands forming a network in the meshes of which is a slightly coagulable, non-corpusculated fluid. This network penetrates everywhere between the epithelial and other cells, it surrounds the muscle fibres and even accompanies the branches of the nerve-cells as far as the cuticle where however the nerve fibres end freely. Certain of the cells of the parenchyma have become specialised to secrete the calcareous bodies (Fig. I. *e*), and in these cases the secretion has much the same relation to the cell as the fat drop has to its cell in



adipose tissue. The nucleus of the cell can usually be seen on one side of the calcareous nodule.

There remains one point of great interest in Blochmann's paper, and that is that his researches render it extremely probable that the flame cells (Fig. I. *h*) of the excretory system are derived from the external epithelial cells and not as is often thought from the cells of the parenchyma. Careful preparations through the growing region of a *Taenia* show that the flame-cells are not formed by a parenchyma-cell fusing with the wall of one of the excretory canals, and so acquiring an outlet, but that they grow from these canals, pushing their way into the parenchyma. Thus Pintner's comparison between the flame-cell and a unicellular gland-cell, and between the excretory canal and the duct of the gland cell receives material support. This view of the external origin of the flame-cells is confirmed by the ectodermal origin of the excretory system in *Discocelis tigrina* described by Lang.

The interesting discovery of transverse commissures connecting the lateral nerve cords in Tapeworms has just been announced. Mr. Tower,<sup>1</sup> to whom we owe the discovery, studied two species of *Moniezia*, *M. expansa* and *M. planissima* both from the small intestine of sheep. He obtained the best results by using von Rath's preserving fluid, which stains the nervous tissue a greyish blue, and the muscles brownish, the connective tissue remaining lighter in colour than either.

Each lateral nerve cord swells out into a ganglion (Fig. II. *f*) at the posterior end of each proglottis, just behind the level of the transverse excretory canal. The ganglion consists of two kinds of ganglion cells, large and small, and gives off externally several fine nerves, of which one runs forward and is called by Tower the marginal nerve (Fig. II. *e*). The most important branches which arise from the ganglion are, however, a dorsal and a ventral one which traverse the proglottis and end in the corresponding

<sup>1</sup> *Zool. Anz.*, xix., 1896, p. 323.

ganglion of the other side (Fig. II. *a* and *b*), thus forming a complete ring round the body. The dorsal branch is further connected with the ventral by a small commissure situated just within the lateral excretory canals, which are thus in the posterior region of the proglottis surrounded by a nerve ring. Further, both the dorsal and the ventral commissures bear two small ganglionic enlargements (Fig. II. *g* and *h*) each of which gives off a small branch passing forwards and apparently ending—though there is still some

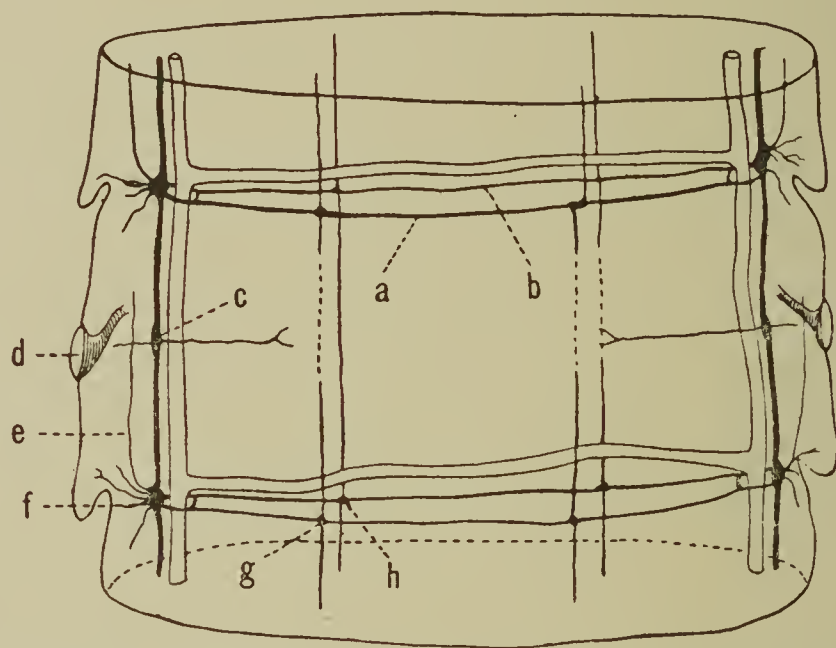


FIG. 2.—A diagram to illustrate the nervous system of *Moniezia* after Towers.

- a.* Dorsal commissure.
- b.* Neutral commissure.
- c.* Anterior lateral ganglion giving off internal and external genital nerves.
- d.* Genital pore.
- e.* Marginal nerve.
- f.* Posterior lateral ganglion.
- g.* Left dorsal ganglion.
- h.* Left neutral ganglion.

doubt as to this—in the corresponding ganglion of the preceding proglottis.

Each lateral nerve cord in addition to the large ganglion at the posterior end of the proglottis (posterior lateral ganglion) also bears a small ganglion about the middle of the length of the proglottis near the genital pore (Fig. II. *c*). This anterior lateral ganglion gives off an internal genital nerve which supplies the ovaries and uterus and an external genital nerve which is distributed to the region of the genital orifice.

Tower's account of the nervous system in the Tapeworm proglottis is by far the most complete that we have



at present, but it must not be forgotten that others have seen at least one transverse commissure in each proglottis. Towards the end of his paper on the "Valves in the Excretory Vessels of Taenias" Kohler<sup>1</sup> describes in *Taenia expansa* a transverse nerve commissure connecting the lateral nerve near the posterior end of each proglottis. This commissure corresponds in position with the dorsal one in *Moniezia*.

Riehm and Zschokke have also described nerves passing transversely from the lateral cord, near the posterior end of the proglottis, towards the interior, but they failed to trace them right across, and in fact in the species they worked at the commissure may be incomplete.

ARTHUR E. SHIPLEY.

<sup>1</sup> *Zeitsch. wiss. Zool.*, vol. lvii., 1894, p. 385.

## TERATOLOGY IN MODERN BOTANY.

MALFORMATIONS have long played an important part in botanical literature. On the one hand, every variation from that which we recognise as the regular form (which, on that account, is naturally regarded as the normal one) excites our interest, and on the other hand, we are enabled to obtain, by the study of these malformations, a deeper insight into the homologies of the organs, and especially those of reproduction of the higher plants. As I have dealt with this point elsewhere<sup>1</sup> I will not enter further into it here. For this period of Teratology belongs essentially to the past. The present has turned its interests to other questions. We ask rather now, what gives rise to these malformations, and what is their bearing upon the great problems of the origin of the organic forms?

In endeavouring to indicate shortly the most important contributions which have been made to the solution of these questions, I must lay stress upon the fact that it is not possible to define exactly what constitutes a malformation. No line of demarcation can be drawn between malformation and variation, though one would be inclined to lay it down as does Darwin,<sup>2</sup> that "by a malformation is understood any important modification of the structure of such a kind as to be disadvantageous or even useless to the species".

### I.

How do malformations arise?

In attempting to answer this question, we encounter a serious difficulty at the very outset. Whilst we see that on the one hand they may be caused by definite external lesions, on the other there is a mass of evidence to show

<sup>1</sup> See "Entwicklungsges. d. Pflanzenorg., *Schenk's Handbuch*, iii., 1.

<sup>2</sup> *Entstehung der Arten*, p. 63, German translation.



that malformations may be hereditarily transmitted, that is to say, they may proceed from internal causes with which we are unacquainted. Instances of the latter kind have been partially known for a long time. It is a matter of common knowledge that the doubling of flowers may be perpetuated by seed, as may also the remarkable appearance of peloria in many plants (see Darwin, *Variation of Animals and Plants*), and even that in some cases constant races have been obtained which always produce certain malformations. This is the case in *Celosia cristata*, the well-known Cockscomb. In the plants with which I experimented, my experience was opposed to that of other authors, for I found that the transmissibility of the fasciation by heredity is absolute. Even when I cultivated the plants in sterile sand, they always exhibited this phenomenon, even in the second generation.

Transmissibility by heredity, at any rate partial, may be assumed for all such malformations as arise spontaneously. Evidence in favour of this is afforded by the investigations of De Vries.

1. *Fasciation*.<sup>1</sup>—De Vries was able to demonstrate the hereditary transmissibility of fasciation in eight plants, though it was never so absolute as to be exhibited by every individual, but still the fact that it did occur was plainly shown. As an example may be taken *Crepis biennis*, in which fasciation was shown in the radical inflorescences

in the second generation in	-	-	30 per cent.
in the third generation in	-	-	40 per cent.
in the fourth generation in	-	-	30 per cent.
in the fifth generation in	-	-	24 per cent.

Sometimes, too, a generation may be missed. Thus the seed from two fasciated flower-heads of *Taraxacum officinale* when sown gave, in the first year, only normal individuals, but in the second year the same plants showed ten fasciated inflorescences, and this increased to about 30 per cent. in later generations. External influences are

<sup>1</sup> De Vries, "Over de erfeligkheid der fasciatien," *Botan. Jaarb.*, Dodonala, 6, Jaarg., 1894, with résumé in French.

apparently of considerable importance. Only well-grown and well-nourished specimens showed the fasciation, and this agrees with facts to be referred to later.

2. *Forced twisting*.<sup>1</sup>—By “forced twisting,” A. Braun understands the form which climbing-plants may exhibit, as a consequence of the distorted growth of the leaves in a spiral line of but little extensibility. This may occur as an abnormality in plants whose leaves are normally disposed in whorls, the leaves taking up a spiral position, growing awry at their bases, and so forming a wreath around the stem.

As the stem elongates, it is forced to unroll this spiral as far as possible, and turns itself in the opposite direction.

By observations made upon a large amount of material De Vries was able to demonstrate the correctness of Braun's views of forced twisting. The only specimens previously available had been those accidentally found in a wild state. As soon as it was proved that forced twisting was hereditary, it became possible to procure numerous examples for purposes of investigation, and also to ensure the production of the abnormality. It was then found that weak seedlings give less prospect of well-marked specimens of forced twisting than strong and well-manured ones, in which, moreover, other malformations, such as increase in the number of cotyledons, fasciation, etc., are more apt to occur.

3. *Hereditary Sterility in Indian Corn*.<sup>2</sup>—In cultivating Indian Corn some of the plants were found to be completely sterile, and unbranched. In this case too, when heredity is in question, the relation must be precisely the same as in plants with double flowers, themselves sterile, but descended from single-flowered specimens, which latter tended to produce double-flowered offspring. An almost sterile plant, the spikes of which bore only very small grains was selected, and 19 per cent. of the offspring proved

<sup>1</sup> De Vries, “Monographie der Zwangsdrehungen,” *Pringsheims Jahrb.*, xx.; and “Eine Methode Zwangsdrehungen aufzusuchen,” *Ber. der. d. Bot. Gesellsch.*, xii.

<sup>2</sup> De Vries, “Steriele Mais as erfelijk ras,” *Bot. Jaarb. Dodonala*, 1890; and “Over steriele Mais Planten,” *ibid.*, i., 1889.



to be quite sterile, whilst of the offspring of other, more robust examples, sterility occurred in only a very few cases.

The experiments of Heinricher<sup>1</sup> must, lastly, be mentioned. He found that a second whorl of stamens which is normally absent when it did occur could be hereditarily transmitted. The precise form of the members of this whorl is, indeed, subject to great variation. The stamens are sometimes stunted, at others fully developed, sometimes they were replaced by staminodes, with or without pollen sacs, at other times they were reduced to mere scar-like structures. Complete fixation, *i.e.*, the cultivation of stocks yielding only six-stamened flowers has not yet been attained. A point of special interest is that flowers also occurred in which the inner perianth whorl was constructed in exactly the same way as the outer one, so that the form of flower in this case presented a great variation from the normal one, and might perhaps be regarded as an exaggerated reversion to an ancestral type.

## II.

On the other hand, a number of cases are now on record in which malformations have been successfully produced by artificial means. We do not include in this category such appearances as result from insufficiency of light, conditions of temperature, and so on. The lower plants, especially the moulds, have proved to be particularly adapted for these observations.

Raciborski has recently produced interesting malformations in *Basidiobolus ranarum*.<sup>2</sup> This mould consists normally of cells containing a single nucleus, which are cylindrical in form and arranged in rows. The fungus is one which can be easily cultivated. If cultures be made in 10 per cent. Glycerine solution, and kept at a somewhat high temperature (30° C.), there are very often developed (though all the cells do not react alike) giant-cells of 60 $\mu$  in

<sup>1</sup> Versuche über die Vererbung der Rückschlagserscheinungen bei Pflanzen," *Prings. Jahrb.*, xxiv.

<sup>2</sup> M. Raciborski, Ueber den Einfluss äusserer Bedingungen auf d. Wachstumsweise d. *Basidiobolus ranarum*.

diameter which contain numerous nuclei, and between these latter in some cases delicate walls are formed. As the concentration of the culture-medium is increased the cells keep on diminishing in length and approach the spherical form, whilst the walls assume, with increasing frequency, an oblique or even longitudinal direction instead of a transverse one, this never happening under normal conditions. We here meet, apparently, with fundamental disturbances of growth; the giant-cells are no longer capable of multiplication, but eventually die out. Other abnormalities will not be referred to here, except to state that by cultivation in 1 per cent. ammonium sulphate or 10 per cent. ammonium chloride *Basidiobolus* may be compelled to pass through a "Palmella stage," which is unknown in the case of any other mould. It isolates itself as spherical cells with thick walls, and these free themselves from the old cell-envelope. The interference with development is clearly more limited in this instance than in that of the giant-cells above described.

Similar results have been obtained in the case of some algæ; in these, too, abnormalities may be produced by the composition of the culture-medium, especially as regards its concentration, though they do not go so far as in *Basidiobolus*. Thus, Chodat and Huber found<sup>1</sup> that in *Pediastrum Boryanum* the formation of daughter-colonies does not occur in concentrated culture-media, and the cells sometimes become metamorphosed into large "hypnocysts"; Richter<sup>2</sup> has also seen abnormalities occur in other fresh-water Algæ when cultivated in salt solution.

In passing on to the Phanerogams I would repeat, in the first place, the words with which a distinguished investigator on the etiology of malformations, Peyritsch, opens his treatise upon the origin of the formation of peloric flowers. He says: "In studying the cause of the formation of peloric flowers, and especially in reference to modifications of structure, two points must be kept in mind. One refers to *causation*;

<sup>1</sup> "Recherches experimentelles sur le *Pediastrum Boryanum*," *Bull. Soc. bot. Suisse*, 1895.

<sup>2</sup> Ueber die Anpassung der Süßwasseralgen an Kochsalzlösung," *Flora*, p. 4 ff., 1894.



and it implies that although in many cases the agent is an external one, there is an internal factor also, that is to say, a predisposition to the production of the anomaly. One may convince one's self by experience that all individuals of a given species do not react to an external influence of an unfavourable character in the same way at all times, nor is the capacity to vary or to appear under abnormal forms, to suffer from disease, equally present in all in the same fashion."<sup>1</sup> And the experiments of De Vries, above referred to, lead to the same conclusion.

For our present purpose it is indifferent whether peloric flowers be regarded as malformations or as examples of "reversion to type". Without doubt the radial forms of inflorescence represent an earlier type of flower-disposition than the dorsiventral (zygomorphic) flowers which are normal to the plants referred to.

As regards the etiology of peloria it is known that when flowers are developed at the apices of stems the remainder of the flowers upon which are zygomorphic, these apical flowers are, almost without exception, radial (peloric), but laterally situated flowers *may* also develop as peloric ones. The influence of position upon zygomorphy is thus here unmistakable, though the attempt to prove this by strict experimental methods is an exceedingly difficult task. Thus, although Hoffman<sup>2</sup> endeavoured to produce peloric flowers in *Achimenes grandiflora*, *Salvia Horminum*, *Gloxinia speciosa*, and others, the negative results of these experiments would seem to have been a foregone conclusion, made, as they were, by causing the flower-buds to assume a vertical position artificially. By the time that the flower-buds, zygomorphically arranged, are amenable to treatment, their development has advanced to such a point that it is useless to expect any modification of importance to take place. Hence Hoffmann's experiments are scarcely capable of being employed for critical purposes, numerous though they were.

Peyritsch, in his work already referred to, endeavoured

<sup>1</sup> *Denkschriften der K. k. Akad. Wien*, bd. 38, 1878.

<sup>2</sup> *Botan. Zeitung*, p. 625, 1875.

to arrive at the immediate cause of the formation of peloria by other means. Starting from observations made upon wild plants he asked himself whether the formation of peloria might not be determined by a change in the conditions of life. Experiments with *Galeobdolon luteum* and *Lamium maculatum* seem to indicate that this is actually the case. These experiments, it is true, leave many important questions unsolved, but I mention them the more readily in this place since an extended repetition of them is greatly to be desired.

In their natural habitat the Labiates just mentioned grow in the shade of other plants. If the latter be removed, as, for instance, by the clearance of wood in forests, many peloric flowers, accompanied by other abnormalities, make their appearance. It is thus reasonable to assume that the increase in the intensity of light acts as the proximate cause of these malformations, and the view that changes in the conditions of life cause plants to vary is thus clearly supported. Plants were then exposed to a stronger illumination, and although control-experiments, made by dividing the stocks and placing a portion of the plants in normal (shady) situations, were unfortunately omitted, it was found that some specimens failed altogether to develop flowers; in one case the time of flowering was altered, and the flowers were borne on shoots which do not normally carry them, whilst three examples produced terminal peloric blossoms. Two specimens were nearly normal, but even in these the proportion of the floral leaves was abnormal in one flower.

In the following year the abnormal appearances were less marked. The plants seemed, so to speak, to have grown accustomed to their new conditions of life; and although the production of flowers was lessened, this was doubtless due to the unfavourable influences operating upon the growth as a whole. Similar anomalies occurred in *Lamium maculatum*, though, as in *Galeobdolon*, these never extended to the whole number of plants. Abnormalities occasionally occurred in the vegetative region, but all the plants did not react alike. It must be mentioned here, and



indeed the fact has already been referred to, that in a number of plants, *e.g.*, *Digitalis purpurea*, the tendency to the formation of peloria is transmissible by seed, and Peyritsch relates a similar case in *Leonurus cardiaca* among the Labiatae. In *Galcobdolon* and *Lamium*, however, the tendency (which must be here regarded as a latent disposition) to the formation of peloria only shows itself when special conditions of life call it forth. In this connection an example may be mentioned which does not indeed belong strictly to teratology, but which shows that there may be present in a plant two different organ-forming tendencies, of which the one is in a latent condition at a certain stage in the life-history of the plant, but may be brought into action by the operation of external factors. Many swamp-loving monocotyledons first produce lanceolate primary leaves,<sup>1</sup> whilst later they bear more highly developed leaves with stalks and blades. A plant of *Sagittaria natans* or *Eichhornia azurea* may, however, be compelled to repeat the formation of the simple leaf by merely placing it under unfavourable conditions, by cutting the roots, for example, or by immersing them in distilled water. The power to form these early simple leaves is thus proved to have been still latent, and although the plant had long been producing other leaves, stimulus from without brought this power into activity again.

In a similar way we can explain the fact that fasciation may be artificially produced by causing the sap to pass rapidly and with increased intensity into a lateral bud which would normally receive but a small quantity of nutriment may be readily produced in some annual plants (*Phaseolus multiflorus*, *Vicia Faba*) by cutting off the main axis above the cotyledons. The axillary buds frequently then become fasciated instead of developing normally. In the same way I was able to cause the simple primary leaves of *Vicia Faba* to develop into foliage leaves, or into such intermediate forms between foliage and primary leaves as any teratologist would recognise as malformations, and in experiments in-

<sup>1</sup> See Goebel, *Pflanzenbiol. Schilderungen*, vol. ii.

stituted by A. Mann at my suggestion, he succeeded partially in effecting a like transformation in *Pisum sativum* in all these cases the effect was due to definite material causes, and we are justified, therefore, in assuming that a similar cause operates when the malformations are caused by animals or by parasitic moulds. I confine myself to the former, since such causes have received far less attention than those of the latter class.

The experiments of Peyritsch on the production of double flowers and other variations of structure by artificial means are of special interest.<sup>1</sup> Unfortunately the death of the investigator has rendered it impossible for him to give the full results of his experiments in detail, and we possess only the short communication referred to along with another<sup>2</sup> in which the author showed that by infecting species of *Arabis* with species of *Aphis*, chloranthy may be artificially produced, provided that the development of the buds selected for the operation be not too far advanced. The chloranthy was accompanied by interference with the development of the sexual organs, the pollen in particular being rudimentary, and apparently incapable of performing its function.

More pronounced malformations were produced by the infection of other plants, *e.g.*, some Valerianaceæ and Cruciferæ, with *Phytoptus*. These consisted partly of abnormalities in the leaves, and partly in various kinds of double and proliferating flowers. The first group generally consisted in the arrangement of the teeth of the leaves in a comb-like manner on leaf flaps which projected considerably beyond the general outline of the leaf. In *Centranthus calcitrapa* this appearance often took the form which Masters in his *Vegetable Teratology* (p. 445), describes as "Enation of leaf-organs".

In the inflorescences of Cruciferæ the bracts to the flowers which are usually absent (aborted) in this order

<sup>1</sup> "Sitzungsber. der Kais. Akad. d. Wissensch. in Wien," Bd. xcvi., 1888.

<sup>2</sup> "Aetiologie der Chloranthien einiger Arabis-arten," *Pringsh. Jahrb.*, xiii., 1.



frequently appeared in connection with several of the flowers and resembled small foliage-leaves in form and texture. Again, the doubling of the flowers occurred in the most various ways, all intermediate stages between the conversion of odd stamens and carpels into petals, and complete doubling being represented, and some flowers further had double, some treble corollas and calyces. And besides this, fresh shoots were also observed in the interior of some of the flowers.

All these effects were produced by inoculation with a parasite, a *Phytoptus*, which occurs in aborting buds of *Valeriana tripteris*. The degree of metamorphosis was not the same in all cases, but varied with the strength of the infection, and with the sensitiveness of the plants.

Two points in these experiments appear to me to be of special significance. The one is the fact that, as in the formation of galls, the malformations are due to a direct action on the part of the parasite, and secondly, that in the process there is no formation of new organs, but rather an interference with any such formation.

This statement may appear at first sight too sweeping, wanting in clearness, and doubtful, but I consider it as representing the correct position, and I will go on to support it by some examples. When a flower becomes green the foliage-leaves which supersede the petals, stamens, and so on, take the form of the ordinary foliage-leaves of the plants, *e.g.*, in *Drosera* it is even found that the chloranthic blossoms have upon their leaves the characteristic tentacles. The chloranth is, indeed, not always perfect, and the forms of the leaves which result from it are then simpler, but the extreme cases give very clear indications of the general nature of the process. Moreover, when flowers become double and new petals are formed, the latter have the same form as the ordinary ones, in accordance with the principle just laid down. The malformation consists in an abnormal metamorphosis, and to a certain extent in *pot pourri* of the various organs. But as in the development of galls no histological components which are absent from the plant make their appearance, so, in these malformations,

no new morphological element is to be found. The *combination* of already existing properties is new, but the properties thus combined remain themselves constant, like the fragments of coloured glass which give rise to the changing pictures of the kaleidoscope. Malformations resulting in the formation of compromises between two organs are the very frequent consequence of this, thus Peyritsch has observed in *Valeriana* all intermediate stages *between* bracts and pappus-rays instead of bracts only, and the same between bracts and petals.

If then nothing new arises during such malformation, but only another combination of parts already present, we are justified in concluding that it is necessary to be cautious in assigning phylogenetic significance to malformations as has very often been done. Admitting that many of the latent capabilities which exist in plants are called into action in an augmented degree by malformation processes, the question is only one of the revelation of something which was really existent though in an attenuated condition, and not of a change in the organs as a whole. This occurs when, for instance, leaflets appeared instead of ovules in chloranthic flowers. The characteristics of ovules, the embryosac, and so on, have disappeared. But, on the other hand, when the *bracts* of the inflorescence of a Crucifer, for instance, are developed, this may, upon comparative grounds, be regarded as a reversion to type. The same is true of the fact observed by Treub and others, that when gall-formation occurs in the flower-heads of *Hieracium umbellatum*, Calyces in all stages from the normal pappus of the flower to the occurrence of five separate green leaflets with regular venation were found. But such an inference can only be justified by comparison with allied forms, since it is probable that there are also latent tendencies which were never developed in the ancestral forms.

Thus, in *Selaginella pentagona* A. Braun and Strasburger have noted remarkable gall-formations, externally resembling bulbils. These have six rows of similarly formed leaves, whilst, as is well known, the leaves of *Selaginella* are nor-



mally arranged in four rows, the leaves in two of the rows being much smaller than those in the other two rows. An arrangement of leaves such as is exhibited in these gall-bearing shoots (which are inhabited by the larva of a Dipterous insect) is never found in *Selaginella* under other circumstances. The bulbils grow with a triangular pyramidal apical cell. The first stages in their development are unfortunately unknown, but they probably begin as outgrowths on young shoots as a result of the irritation produced by the larva.

A similar instance is afforded by the singular "witches brooms," which are formed upon the leaves of *Pteris quadriaurita*, as the result of the action of a mould, *Taphrina cornucervi*. These are adventitious shoots with misshapen leaves; adventitious shoots do not normally appear upon the leaves of the plant in question.

The malformations, resulting from the action of animals already alluded to, lead us to glance at the latest observations upon the origin of galls. It is not surprising that these curious structures should have attracted attention at an early period. We see here that, as the result of irritation applied by an animal, there arises a new growth which is admirably adapted to afford food, dwelling, and shelter to the creature therein developed. What is the nature of this stimulus? In the opinion of Lacaze-Duthiers,<sup>1</sup> with which Darwin and Hofmeister also concur, a poisonous substance is introduced by the insect when laying the egg by means of its ovipositor, and that this gives rise to the formation of the gall. It is evident that the irritation to which the parent insect gives rise presupposes a power of responsive action; the virus of *Cynips rosæ*, for example, is destitute of action upon the oak, which nevertheless so readily produces galls under appropriate stimulation.

As has, however, been shown by the well-known entomological researches of Adler, the theory enunciated by Lacaze-Duthiers cannot be regarded as trustworthy. In the department of botany our knowledge of the formation

<sup>1</sup> "Recherches pour servir a l'histoire des galles," *Ann. Sci. Nat. Bot.*, 1853.

of galls has been greatly added to by Beyerinck.<sup>1</sup> It was found that in galls produced by Cynipidæ, the stimulus which determined the gall-formation did not proceed from the parent, but from the larva. The influence of the latter is exerted even whilst still contained within the egg as is proved by the simple fact that in many cases the eggs are deposited on the surface of the young organs of plants and cemented there, and are then surrounded with a wall by the adjacent tissue. This can only be explained upon the supposition that the larva secretes soluble substances, and that these enter the tissues of the plant. Again, the larva has often been removed from the growing tissue which is being converted into the gall, and indeed in some cases has been separated from the growing tissue by dead tissue, without influence upon the growth of the gall. This shows that the case with which we have to do is not one of propagation of the irritation, assisted by the living protoplasm of the host. Moreover, since the action is a slow one and proceeds from the larva, it may be arrested by killing the latter. Since their growth is interfered with at those points of the young tissues which are in immediate contact with the animal, there is formed a chamber which is always lined with nutriment at the disposal of the larva. As regards the theory of gall-formation, the fact discovered by Adler is of great importance, confirmed as it has been by Beyerinck, that upon one and the same host, the oak, the various forms of a single species of gall-insect produce various galls. The female insects of *Dryophante folii*, for instance, emerge from their galls upon an oak-leaf in November or December. They immediately look for a bud, a "resting eye," and deposit an egg upon its vegetative point, a small violet-coloured bud-gall resulting, which, before the connection was known, was ascribed to a gall-insect known as *Spathogaster Taschenbergi*. The males and females of this species leave their dwellings in May, and the fecundated female insects deposit their eggs in the veins of young oak-leaves and thereby give rise to the leaf-galls with which we started.

<sup>1</sup> "Beobachtungen über die ersten Entwicklungsphasen der Cynipidengallen," Amsterdam, 1882.



The two galls differ both in form and in histological structure. Does this arise from the fact that the substance secreted by the parthenogenetic eggs (which substance determines the gall-formation) is a different one from that formed by the impregnated eggs, or is it due to a difference in reaction between the vegetative point and the leaves? The reply to this question is, in my judgment, of far greater importance than the investigation of apical cells and other minute histological details on which so much labour is being expended.

We have already referred to the admirable adaptation of the galls to the requirements of the larvæ, and a point of special interest is that the animal is also protected from enemies during its development, partly by mechanical means, partly by chemical ones (especially the abundant formation of tannin), though the fact that this protection is by no means absolute is shown by the frequent attacks to which the galls are subjected.

The protection required is in other cases effected as the result of the irritation caused by the larva in the shape of the formation of roots which overgrow the larval chamber, and by becoming fused together forming a close living mantle. This is the case with the gall which *Cecidomyia Poæ* causes upon *Poa nemoralis*.<sup>1</sup> The roots in this case arise at points at which they normally are never found. Here the irritation which leads to the formation of the gall proceeds from the larva, which attaches itself firmly to the surface of a still-growing internode; fold-like swellings first appear at a considerable distance on either side of the larva, and the roots arise from these swellings, and may be made to develop into normal roots if the gall be used as a slip or cutting. The behaviour of *Nematus capreæ* however shows that the gall is not always formed *entirely* as a consequence of the action of the larva. The old theory of Lacaze-Duthiers here applies, the development of the gall depending upon the substance which is introduced into the young leaf with the egg from the poison bag. This is clear from

<sup>1</sup> Beyerinck, *Bot. Zeitg.*, p. 305, 1885.

the fact that every wound caused by the saw of the insect gives rise to a gall, even when no egg is laid, and further, that the artificial destruction of the egg does not prevent the formation of the gall, the development of the egg determines only the size of the gall.

In concluding this short account of the latest researches into the formation of galls, two points alone need be adverted to. The one is, that in the anatomical structure of gall generally, no new tissue-components appear other than those which the plant attacked already possesses, though they exist under other conditions as regards situation and distribution. The other is, that all the more highly-differentiated galls spring from young tissues still in course of development, these being caused to assume abnormal structure as the result of the action of the gall-insect.

### III.

Certain general conclusions which arise out of the preceding facts have already been alluded to, and we may here shortly refer to the theoretical considerations to which they have led. The chief of these is Sachs's theory of "material and form" <sup>1</sup> which has been specially employed with reference to malformations.

Sachs starts with the assumption that the differences in the forms of the organs of plants depend upon differences in their material components, and that the variations in the organic forms result from variations in the processes of nutrition. Thus the substances which give rise to the formation of a foliage-leaf are different from those which lead to the formation of a carpellary leaf. If this be so, the causative action of the so-called morphological processes may be admitted, just as in the instance of the morphology of a crystal. We can then form a mental picture of the way in which it happens that in malformations, one organ so frequently appears in the place of another, or that the relative forms of the two organs are commingled in the

<sup>1</sup> *Gesammte Abhandl. über Pflanzenphysiologie*, J. v. Sachs, ii., 1156 ff.



strangest fashion, just as are the peculiarities of two different species in their hybrids.

The malformations caused by animals show us, as a matter of fact, that the development of organs is modified by material influences, although, as has been said, the range of those modifications is naturally limited by the peculiarities of the particular plant. The fact that they are of such frequent occurrence in the flowers, and relatively rarely are found in the roots, for example, may be due to the following peculiarities :—<sup>1</sup>

1. The organs arise at the vegetative point of the inflorescence in rapid succession, and usually in considerable number, close above and by the side of each other.

2. There are thus formed at short intervals organs of varied structure, *e.g.*, petals, stamens, etc.

3. Comparatively slight disturbances would thus suffice to call forth changes in the arrangement as the organ-forming materials are supplied, since the normal development of parts of so complicated a character can only occur when the supply of material and the phenomena of cell-division occur with almost mathematical exactitude. If, for example, a few molecules of the material which gives rise to the growth of anthers were diverted to the right or left to the extent of the thousandth of a millimetre, or were to be delayed or accelerated upon their journey in the apical region of the inflorescence, the characters of a stamen might be partially assumed by a petal or a carpel.

During my researches into the development of double flowers,<sup>2</sup> I was led to the conclusion that Sachs's theory offers really the simplest expression of the facts. In all these cases the question is one of increase in the quantity of the materials out of which the parts of the flower are formed. This finds expression at one time in the cleavage of the normal layers of the parts, at another in the appearance of new whorls, and again, in the conversion of

<sup>1</sup> Compare Sachs, "Ueber Wachstumsperioden und Bildungsreize," *Flora*, p. 217, 1893.

<sup>2</sup> Goebel, "Beiträge zur Kenntniss gefüllter Blüten," *Pringsh. Jahrb.*, xvii., p. 207 ff.

other whorls in the flowers into petals, and with these disturbances there are connected numerous and far-reaching ones in the structure of the composition of the flower as a whole.

Beyerinck<sup>1</sup> has been led to similar conclusions to those of Sachs upon the question of the formation of galls. He assumes that the substance secreted by the animal possesses the character of an enzyme, and that there are "enzymes of growth," which so effect the protoplasm of host that gall-formation results. Beyerinck assumes similar enzymes of growth in normal development of organs, only that in this case they are produced by the protoplasm of the plant itself. Since these enzymes must apparently be different for each organ, his theory very nearly approaches that of Sachs.

We must, however, be satisfied with this short account of the general question. And although the preceding exposition may be far from affording an exhaustive account of the matter, it may yet suffice to show that whilst the object and method of teratology in modern botany have changed, the subject has not lost anything of its interest or importance, rather the reverse.

K. GOEBEL.

<sup>1</sup> *Botan. Zeitg.*, 1888.



## THE NERVOUS SYSTEM OF CŒLENTERA.

SINCE Oscar and Richard Hertwig published their extremely valuable monograph on the sea-anemones, when the nervous system both in the ectoderm and the endoderm of these animals was for the first time accurately described, a series of important papers has been published both at home and abroad confirming their general results and extending them to other groups of Cœlentera. The anatomical details of the nervous system of a group of animals which must still be regarded as the most primitive of all Metazoa naturally excites the interest of all zoologists and physiologists. The complicated nerve ganglia and cords of Chætopoda, Arthropoda, Mollusca and Vertebrata are in nearly all cases situated in the mesoblastic tissues of the adult. The teaching of embryology points undoubtedly to the ectoderm or epiblast as the source from which this nervous system is derived. Therefore must we look to those animals which do not possess any mesoblast at all if we wish to learn more about the original form the nervous system of animals possessed.

In the higher Metazoa the greater part of the nervous system is not difficult to discover.

The greater ganglionic enlargements, and the bundles of nerve fibres forming nerve cords from which the finer branches pass to the muscles and the organs of sensation, stand out clearly from the surrounding tissues. But in some forms, such as Nemertine worms, Platyhelminthes and in the embryonic stages of many others, including several Vertebrata, the main trunks of the central nervous system not only give off definite nerve fibres to definite organs or tissues but are connected with a loose, spongy plexus of fibrils and cells which spreads through the tissues in a manner that it is difficult to fully map out.

In most cases such as Palæonemertines, Nematoda, Tadpoles, etc., this plexus is situated immediately below but continuous with the ectoderm, and it is reasonable to

suppose that it is homologous with the ectodermic nervous system of the Cœlenterates.

Regarding the nervous systems of these animals from a general standpoint, we notice that they differ from the Cœlenterates in two particulars. Firstly, in the presence of certain ganglia are tracts of nerve fibres in addition to the subectodermic plexus of nerve cells and fibrils, and secondly, in the fact that the endodermic nervous system is either absent altogether, or else that it is so poorly represented that it has hitherto escaped observation. (The plexus of Auerbach and Meissner in the alimentary canal of Vertebrates may represent the endodermic nervous system, but so far as I am aware there is no embryological proof of this at present.)

The predominance of the ectodermic nervous system in the higher animals is readily accounted for by the fact that all the most important sensory impulses must originate in ectodermic tissues and the great muscles which move the body and limbs of the animal are derived from the somatic *i.e.*, the subectodermic layer of the mesoblast. The muscles of the splanchnic layer of the mesoblast which are moved by the endodermic nervous system—if such a system is really present—are comparatively slight, and the sensory impulses of the endoderm, although important physiologically perhaps, are general rather than special in character.

Two important questions have now to be considered. Firstly, do the plexus and the fibrils situated in the ectoderm of Cœlenterates really perform the same or similar functions as the epiblastic nervous system of the higher animals? And secondly, is there any direct or indirect histological communication between the ectodermic and endodermic plexuses?

In the consideration of the answer to the first question we must remember that the histological similarity of the tissues of two animals is not a conclusive proof that they perform the same functions. To prove that any system of cells and fibrils is nervous in function we must have physiological evidence that they originate, reflect, or transmit



nervous impulses. In the higher animals it is not difficult to obtain such physiological proofs of the functions of the nervous tissues but in most Cœlenterates where these tissues are extremely minute and diffused over a wide area the proof is not so easy to obtain.

A series of observations and experiments made last year by Hesse seem to afford the necessary proof of the nervous character of the ectodermic nerve plexus in certain Scyphomedusæ, and consequently mark a very important step in advance.

At the margin of the umbrella in these animals there may be seen a small number of very minute and extremely modified tentacles called the tentaculocysts.

These organs have been shown by Romanes and by Eimer to be the centres from which the impulses controlling the movements of the bell proceed, and from this fact, and others which it is not necessary for our purpose to refer to, they are frequently spoken of as the "sense organs" of the medusa. When all eight of the sense organs of an *Aurelia*, for example, are removed, the rhythmic contractions of the bell cease altogether, if one or any greater number are left intact the contractions continue. If the margin of the bell with one or more tentaculocysts be removed it continues to contract, whereas the remainder of the bell from which the margin has been removed ceases to contract. These and other experiments together prove that the nerve centres originating and controlling these contractions reside in the sense organs. Now on the inner, and in some genera on the outer, surface as well of the base of the tentaculocyst there is situated a pit, and it is a well-known fact that at the base of these pits there is a considerable thickening of the subectodermic layer of cells and fibres which is commonly called the "nerve sheath".

Hesse shows that the thickening of the subectodermic nerve plexus in each inner pit gives origin to several very much elongated bipolar ganglion cells, which run in very definite tracts. Passing from the sense organ immediately below the subumbrellar epithelium they form a bundle of fibres running in a radial direction towards the centre of the

bell. After a short course in this direction these elongated cells bend at right angles and form together with similar cells proceeding from other sense-organs a circular band of fibres, which completes the circuit of the bell. In connection with these circular and radial nerve tracts there are bundles of muscular fibres arranged in a regular and rather complicated manner, and there seems to be little doubt that the rhythmic contraction of these fibres causes the rhythmic contraction of the bell as a whole. It cannot be said that Hesse's observations on these histological points are altogether novel. Claus, Eimer, Schäfer and others have partially described them before, but with the help of more modern methods of research Hesse has been able to give us a more complete and satisfactory description than any of his predecessors.

Without referring to further details of the distribution of this important nerve plexus we may now, in view of the physiological experiments to be described, consider it to be proved that the so-called nerve sheath of the inner sensory pit of the tentaculocysts is continuous with bundles of fibres—or elongated bipolar ganglion cells; that these fibres run radially from the margin and then circularly to form a broad tract, and that finally these tracts are confined to the subumbrellar aspect of the bell.

It can be shown that if semicircular incisions be made through the subumbrellar epithelium round each of the tentaculocysts, so as to cut through radial tracts, the effect is the same as if the tentaculocysts were entirely removed, that is to say, the rhythmic contractions cease. Moreover if the epithelium of the base of the tentaculocyst itself be severed the effect is the same. On the other hand if the epithelium on the upper side of the ball be cut in a similar manner and with it the subjacent mesogloea the contractions continue, so long as the subumbrellar epithelium is intact.

These experiments prove then conclusively that the nervous impulses which stimulate and regulate the movements of a medusa traverse the subumbrellar epithelium only in definite directions, which correspond with tracts of



the cells and fibres previously described as nervous from histological appearances,

It is not probable that we shall be able to prove in a similar conclusive manner that the "nervenschicht" of the Hydroids and of the Anthozoa has the same function, but nevertheless these experiments give us much more confidence in the assertions that are made as to its nervous function.

Mention was made at the commencement of this essay that in sea-anemones and other Cœlenterates the nerve plexus is not confined to the ectoderm, but that similar cells and fibres may be found in connection with the endoderm.

The brothers Hertwig have described and figured this endodermic nervous system in the sea-anemones, but perhaps the most favourable Cœlenterate that can be readily obtained for its investigation is the *Alcyonium*.

This form consists of lobate colonial masses perforated by tubes—the polype cavities—passing from the surface, where they terminate in the mouths of the polypes, to the base of the colony. These tubes are lined by endoderm. The ectoderm is confined to the general surface of the mass and to the body wall, tentacles and stomodæum of the protrusible portions of the polypes. It would be impossible in such an essay as this to describe the details of the course of these two layers, but it will be sufficient to state that when compared with a Hydrozoan or a sea-anemone, the endoderm is in *Alcyonium* a very extensive and important tissue. The endoderm lining the tubes is provided with a considerable muscular layer—the muscles forming a cylindrical sheath immediately subjacent to the epithelium.

It is now fully recognised that when an *Alcyonium* is removed from the water or irritated in any manner in the water it is capable of contracting in bulk very considerably, and this contraction must be brought about by the cylindrical muscle sheaths expelling a portion of the water in the tubes.

The endodermic nervous system which, we may presume, governs these contractions, may be seen quite clearly

in fresh preparations stained by the Ehrlich methyl-blue method, in the form of a plexus of ganglion cells and branching nerve fibres.

This plexus is in connection with certain branching cells sparsely scattered in the mesogloea, and it seems extremely probable that these in their turn are connected with the ectoderm, although technical difficulties have made it impossible to prove this point at present.

In the Hydrozoa and Scyphozoa the endodermic nerve system can only with much greater difficulty be discovered, and it probable that in the majority of these forms it plays a far less important part than it does in the Anthozoa.

In *Klujostoma* Hesse figures a marked endodermic nerve sheath on the outer side of the canal of the tentaculocyst. This sends short, tag-like processes into the mesogloea in the direction of the outer sense pit. Corresponding with this the thickening of the nerve sheath of the outer sense pit sends tag-like processes into the mesogloea. In the mesogloea of the same region numerous small angular cells are to be seen differing in several peculiarities from the cells found in the mesogloea of other regions. The conclusion seems to be irresistible that at this point there is established a communication between the endodermic and ectodermic nervous sheaths by way of these stellate cells, and the arguments by which Hesse seeks to prove that this is not the case are far from being conclusive.

Apart from this, however, the endodermic nervous system and its connections of the Hydrozoa and Scyphozoa have not yet been satisfactorily investigated and it is to be hoped that before long some one will with the new methods undertake a thorough investigation of the structure of the endoderm of these animals. The facts of the Cœlenterate nervous system which may now be considered to be established are these. That a plexus of fibres and cells occurs in both ectoderm and endoderm similar in structure and probably similar in function. In some Cœlenterates such as the Scyphozoa, the Ctenophora, many Hydroids, and the Sea-anemones, the ectodermic nervous system is the predominant one as it is in the Cœlomata, but in some of the



colonial Anthozoa, such as *Alcyonium*, it is the endodermic nervous system which is the predominant one. A communication exists between the ectodermic and endodermic nervous systems in the Anthozoa by way of a loose plexus of cells and fibres, but to what extent this also occurs in Hydrozoa and Scyphozoa we have at present but little evidence.

SYDNEY J. HICKSON.

## PALÆOBOTANY AND EVOLUTION.

THE geological history of existing classes of plants is still very imperfectly known. The records of the vegetation of past ages are from the nature of the case exceedingly scanty, and it is only under special conditions that it has been possible for plant remains to leave traces of their existence in the stratified deposits of the earth's crust. The much greater abundance of fossil animals, and the better state of preservation of their hard calcareous, silicious, and bony skeletons, have enabled palæontologists to furnish valuable aids to the history of evolution. Some of these contributions from their readily perceived importance and exceptional interest, have long been familiar to every one possessing the most superficial knowledge of Natural Science.

From palæobotanists we have had various attempts to illustrate the progress of plant evolution by means of genealogical trees of the most comprehensive form, starting from a host of supposed algal remains in the older Palæozoic sediments, and culminating through various ramifications in the highest types of plant structure. The data on which it has thus been essayed to illustrate the manner of origin of existing classes of plants, are frequently valueless, and the evidence available hopelessly inadequate for so ambitious an object. In the majority of cases the building up of such imaginary lines of development has tended "to confuse fancy with fact, and to create mere confusion".<sup>1</sup> The acknowledged insufficiency and unscientific foundations of speculations on plant evolution, have tended to an attitude on the part of scientific investigators of extreme scepticism, and to a general mistrust of palæobotany as a factor of primary importance in phylogenetic inquiries.

Although, generally speaking, fossil plants are comparatively rarely found in a condition sufficiently satisfactory

<sup>1</sup> Huxley, *Method and Results*, London, p. 120, 1893.



for accurate determination and diagnosis, they have occasionally been preserved in a manner far more perfect than is the case with fossil animals. The hard parts of an animal may be found in a wonderful state of preservation, but the soft parts have at most left but a faint impression of their outline, and that only in a few exceptional cases. A well-known example of the impression of a soft-bodied animal is that of the Cambrian Medusa, *Medusites Lindströmi*, Nath., from the Eophyton Sandstone of Gothland. With plants, on the one hand, it is possible to investigate the minutest microscopical details in the structure of the most delicate tissues. Putting aside for the present all those records of extinct plants, which consist simply of structureless casts and fragmentary impressions, we have left a mass of material which has led to something more than vague suggestions and fruitless speculation. As the result of the examination of petrified vegetable fragments of the Permo-Carboniferous strata of England, France, Germany, and other countries, contributions have been made towards the solution of phylogenetic problems based on the most solid foundation of fact. It is notorious that those who confine their attention to living forms, have in a great measure allowed their interest to be restricted within the limits of existing organic types. Fossil and living plants have been treated by different methods, and looked at from entirely different standpoints. In recent years, however, botanists, as a whole, have begun to realise the importance of a logical attitude with regard to the unity of the past and present representatives of the vegetable kingdom. There are now, indeed, unmistakable signs of a more general recognition of the lessons to be learnt by means of the better methods of palæobotanical research, and this awakening interest in the investigation of extinct types is likely to be considerably extended. If we endeavour to take a comprehensive view of recent advances in botanical science, it is difficult to ignore the fact that there are few if any discoveries of more far-reaching and general importance than those furnished by palæobotanical investigations. The prospect in this field of work is a particularly

hopeful one, and cannot fail to attract the attention, if not the actual co-operation, of those interested in the broader problems of botanical research.

The examination of fossil organisms has not infrequently led to the recognition of certain characters suggestive of a combination of features now separated in distinct families. Even before the publication of the *Origin of Species*, the existence of generalised, synthetic, or prophetic types had been hinted at, and in more recent times the interest attached to such fossil forms has considerably increased. In searching for the ancestors of living forms we may sometimes arrive at a point where branching lines of affinity converge, and point back towards some generalised pre-existing stock. The recognition of any such synthetic forms, when based on trustworthy evidence, marks a great advance, and furnishes a far more valuable contribution to the history of organic evolution, than does the construction of genealogies which rest to a large extent on pure assumption, and appeal but little to the well-regulated scientific mind. It is true there are to be found in palæobotanical literature generalisations enough based on imperfect data as to the existence of supposed synthetic types; to refer to a plant which is imperfectly known and little understood, as combining in itself the characteristics of distinct groups, is often a convenient method of coming to a conclusion. Fortunately in not a few cases the evidence on which generalised forms have been described is as sound and conclusive as evidence can be.

No better illustration of such synthetic types can be described, than those recently dealt with in a most able manner in the pages of the *Philosophical Transactions* by the late Professor Williamson and Dr. D. H. Scott. In their memoir on the genera *Lyginodendron* and *Heterangium* the authors have contributed to botanical science results of exceptional importance, demonstrating in the clearest manner the possibilities of palæobotanical work when carried out on strictly scientific lines, and aided by a wide and accurate knowledge of the morphology of recent plants. We may best express the nature of those two Palæozoic fossil plants



by quoting the authors' words: "The view of the affinities of *Lyginodendron* and *Heterangium* which we desire to suggest is that they are derivatives of an ancient and 'generalised' (or rather non-specialised) Fern-stock, which already show a marked divergence in the Cycadean direction. Of the two genera *Heterangium* appears to be the more ancient, and certainly stands nearer to the Filicinean ancestry. *Lyginodendron*, while still retaining conspicuous Fern-like characters, has advanced much further on Cycadean lines."<sup>1</sup>

The generic name *Lyginodendron* was proposed in 1843 by Mr. Gurlie for a piece of fossil plant which he regarded as a new form, but did not attempt to describe scientifically. Williamson in 1873 applied Gurlie's term to certain plant fragments which he investigated from the calcareous nodules ("coal balls") of Lancashire. The plant so named by Williamson had been previously described by Binney in 1866 as *Dadoxylon Oldhamium*. Three years later Williamson proposed a new name, *Dictyoxylon*, for Binney's plant in place of *Dadoxylon*, a genus in which the Oldham specimen could not be included. Finally Gurlie's name was adopted, in the belief that this older generic designation had been assigned to a plant identical with the much more perfectly preserved Lancashire examples.

So far all specimens of *Lyginodendron* have been included under one specific name, *L. Oldhamium* Will. The stems of this plant may be readily recognised in transverse section by the characteristic structure of the outer cortex, and by the histological features of the central cylinder and leaf-trace bundles. The plant is monostelic, and in a young stem the stele consists of an axial parenchymatous pith with nests or groups of dark and thick walled cells. At the periphery of this tissue occur several detached strands of collateral groups of primary xylem and phloem, the former consisting of scalariform, reticulate, and spiral tracheæ, with a very little parenchyma, and the latter of thinner-walled elongated elements and parenchymatous cells, with

<sup>1</sup> Williamson and Scott, p. 769.

scattered secretory sacs. Owing to the presence of a zone of secondary xylem and phloem, the primary phloem is usually crushed and indistinct, having been separated from the primary xylem by the interpolation of the secondary vascular tissue. One of the most important characteristics of the primary group of xylem is the position of the protoxylem; the narrow spiral tracheids occur just internal to the outer edge of each xylem group, and thus occupy an intermediate position, enabling us to distinguish a small group of centrifugally developed scalariform xylem elements and a larger group of centripetally developed pitted tracheæ.

Each of the primary strands of xylem and phloem is a leaf-trace, and in a series of transverse sections it is possible to follow a bundle in its passage from the petiole to the central cylinder of the stem. The course of these foliar bundles is especially interesting; each extends through about ten internodes, five internodes being traversed by the leaf-trace as it moves outwards from the periphery of the pith to the edge of the secondary wood, and five more in its course through the pericycle and cortical tissues. A trace-bundle on its way through the secondary xylem consists of a primary strand and an arc of secondary xylem tracheæ, but as it passes further out through the stem tissues the secondary arc disappears and the trace divides into two distinct bundles. Finally in the petiole the twin bundles are frequently reunited. The collateral structure of the leaf-trace is replaced by a concentric arrangement, of the phloem and xylem as the strand reaches the leaf-stalk base.

The secondary vascular tissues met with in practically all stems of *Lyginodendron* consist of radiating rows of pitted tracheæ, separated by numerous large medullary rays, and of narrow phloem cells associated with sieve-tube like elements. Secretory sacs are fairly common in both xylem and phloem rays. In several specimens the characteristic tabular cells of the cambium have been preserved, and there can be no doubt as to the perfectly normal manner of development of the secondary wood and bast. External to the phloem, and constituting the limits of the



stele, there is a multilayered pericycle made up of short-celled parenchyma, containing nests of sclerous cells and numerous secretory sacs. In most cases the pericycle tissues are succeeded towards the exterior by a deep-seated periderm, which arose at an early stage of secondary thickening from a phellogen developed in the pericycle. The extra-stelar region of the stem may be conveniently described as being made up of an inner and outer cortex; the former consists of parenchyma with scattered secretory cells and occasional sclerous nests. The outer cortex presents a very characteristic appearance, being made up of alternate radiating bands of dark sclerenchyma, and lighter-coloured, thin-walled, parenchyma containing secretory sacs. From the peripheral cells of the cortex plint emergences are here and there developed.

Mention has been made of petioles attached to the *Lyginodendron* stems. The nature of these appendages is of special interest as regards the affinities of the plant.

In 1872 Williamson suggested a possible connection between certain structures described under the generic name of *Edraxydon* and the stem of *Lyginodendron*. Subsequently the genus *Rachiopteris* was substituted for *Edraxydon*, and thus the *Lyginodendron* leaves were included among true fern fronds. There is now direct proof that *Rachiopteris aspera* Will. is the petiole of *Lyginodendron*. The form of the ultimate segments of the frond is that long known to palæobotanists under the provisional generic name *Sphenopteris*. The petiole is made up of a ground-mass of parenchyma with alternate radiating strands of sclerenchyma and thin walled tissue at the periphery. Long secretory sacs traverse the inner fundamental tissues, and externally the cortex exhibits gland-like out-growths or emergences similar to those in *Lyginodendron* stems. The vascular bundle of the leaf-stalk is of the typical concentric form, and usually consists of a mass of V-shaped xylem containing several protoxylem groups surrounded by a thin-walled and small-celled phloem. External to the phloem a more or less well-marked pericycle has been recognised, but no distinct bundle-sheath. In addition to the structural

features of the main petiole and its branches, the histology of the leaf lamina has been described in some detail. The veins in the lamina seem to be of the collateral type, and the mesophyll is composed towards the upper surface of closely arranged cells elongated at right-angles to the epidermis, and towards the lower of more loosely disposed and less regular cells. Stomata have also been recognised in transverse sections of these sphenopteroid pinnules.

Finally the adventitious roots of this interesting genus have been thoroughly investigated. In certain regions of the stem adventitious roots are given off on all sides, both from nodes and internodes; their origin is clearly endogenous, and their histological features such as characterise true root structures. The roots, like the petioles, were originally described as a distinct genus, and named by Williamson *Kaloxylon Hookeri*. The stele of the root consists of two to eight centripetally developed groups of xylem with conjunctive parenchyma, alternating with groups of smaller cells, consisting partly of short parenchyma and in part of narrow elongated elements. Surrounding the xylem and phloem is a one-layered pericycle and a layer of stouter cells with the characteristic radial markings of endodermal cells occasionally visible. External to the innermost layer of the cortex, we have a broad zone of lax parenchyma with conspicuous and abundant secretory sacs, and externally a peculiar epidermal layer made of two or three rows of thin-walled cells. Many of the roots examined show a zone of secondary xylem and phloem, formed in a manner essentially identical with the method of development of secondary vascular tissues from a typical root cambium.

Having thus briefly referred to some of the more striking anatomical characteristics of *Lyginodendron*, it remains to describe in a few words the habit of the whole plant and to discuss its affinities with recent forms. So far we are without any satisfactory evidence as to the nature of the reproductive organs. To quote Williamson and Scott's words:<sup>1</sup> "We must, therefore, picture *Lyginodendron* to

<sup>1</sup> Williamson and Scott, p. 743.



ourselves as having a tall, upright stem rising to a height of several feet and bearing somewhat remote, spirally arranged, highly compound, fern-like leaves. The base of the stem, where the adventitious roots were given off, must have been buried for some depth in the earth or mud. . . . The stem is mechanically well constructed, and thus fitted to maintain an upright position while bearing abundant foliage. We have no distinct evidence for any rhizome-like organs, but it is possible that some of the small shoots which are rather deficient in sclerenchyma may have been creeping or subterranean." Certain interesting examples of anomalous structures in *Lyginodendron* stems have been figured and described, but it is impossible to deal with these in the present article.

*Affinities.* The leaf-trace bundle system of the stem agrees in certain respects with that of *Osmunda*. In both genera the stele possesses a ring of collateral primary bundles, and in both there is good evidence for believing that in the lower stem internodes the xylem has the form of a continuous ring enclosing a central pith. Another point of contact between the fossil plant and recent ferns is afforded by the Gleicheniaceae genus *Platyzoma*, in which the monostelic stem possesses a distinct pith. The protoxylem of *Lyginodendron* is of the same type as that of the foliar bundles of recent cycadean petioles, and in some cases also of the stem bundles of Cycads. The term "mesarch," proposed by Solms-Laubach, has been adopted for this particular form of bundle. The characteristic feature of mesarch bundle, is that the protoxylem is not on the inner or outer limit of the primary xylem tracheæ, but occupies an intermediate position between the primary centripetal and primary centrifugal xylem elements.

The secondary wood and bast are similar in a striking degree to the corresponding tissues in cycadean stems. As regards the cortex, the emergences of the peripheral tissues suggest those of *Alsophila* and other recent ferns. Passing to the petiole, we lose sight of the more distinctly cycadean affinities, and find an obvious correspondence with the anatomy of recent ferns. The concentric bundle is clearly

fern-like; the absence of a definite endodermis recalls the leaf stalks of *Marattiaceæ*. The foliage is equally suggestive of ferns in form and structure. In the roots, as regards the primary structure, we have a further illustration of a fern alliance, and especially with Marattiaceous genera. The above comparisons are sufficient to conclusively demonstrate the synthetic character of the fossil genus.

The second form described by Williamson and Scott must be dismissed in a few words. In 1871 certain stem fragments were discovered amongst the well-known material from Burntisland, which were subsequently referred to Corda's genus *Heterangium*. Of this genus we now possess a comparatively full knowledge of two specific form, *H. Grievii*, Will. and *H. tiliæoides*, Will. The central cylinder of the stem consists of an axial mass of primary xylem traversed by anastomosing bands of parenchyma. Towards the periphery of the central region distinct groups of tracheæ may be distinguished, containing protoxylem elements in the position characteristic of mesarch bundles. As in *Lyginodendron*, these peripheral vascular strands are true leaf-traces. There is a clearly marked pericycle, and external to this a wide inner cortex of parenchyma, containing characteristic horizontal plates of sclerous tissue, followed by an outer cortex traversed towards the periphery by radially disposed bands of sclerenchymatous fibres. In most cases the primary xylem and phloem tissues are surrounded by a zone of secondary wood and bast with numerous medullary rays. The species *Heterangium tiliæoides* is especially interesting as exhibiting a remarkably perfect state of preservation of the sieve-tubes with their lateral sieve-plates. The cambium is occasionally extremely well preserved. The petioles and pinnules are similar to those of *Lyginodendron*, but it has not been possible to investigate their structure to quite the same extent.

Again, in its adventitious roots, *Heterangium* agrees closely with the preceding genus. With the exception of the secondary xylem and phloem, the stem of *Heterangium* is "essentially that of a monostelic fern of the *Gleichenia*



type". The occurrence of pitted tracheids, the collateral arrangement of the xylem and phloem in the leaf-trace bundles in their course through the stem tissues, and the differentiation of the peripheral stelar tissues into distinct leaf-trace strands, are features peculiar to *Heterangium* as compared with recent ferns. No great stress should be laid on the much more considerable development of secondary tissue in the fossil genus than in living ferns. *Botrychium* and *Helminthostachys* both illustrate to a certain extent the power of recent ferns to increase by secondary thickening, and the comparison of other Palæozoic types with their nearest living allies has taught us not to attach any great importance to secondary thickening as a character of primary taxonomic value.

It is of interest to note, that in *Heterangium* the resemblance of the secondary vascular tissues to those of Cycads extends to details of the sieve-plates.<sup>1</sup>

Williamson and Scott have clearly shown that in different parts of their structure the two genera *Heterangium* and *Lyginodendron* reveal distinct points of agreement with *Gleicheniaceæ*, *Osmundaceæ*, *Marattiaceæ*, *Ophioglosseæ*, and *Cycadaceæ*. Without suggesting that these Palæozoic types are the actual ancestors of existing Cycads, the authors regard them as "derivatives of an ancient and 'generalised' Fern Stock, which already shows a marked divergence in the Cycadean direction". The two plants described above, with other genera previously known, clearly point to the existence of a fossil group of plants "on the borderland of ferns and *Cycadaceæ*".<sup>2</sup>

It would be easy, did space permit, to discuss the structure and affinities of several of the Palæozoic plants belonging to this generalised group. The genera so ably and lucidly dealt with in Williamson and Scott's splendid memoir, afford excellent examples of the data which palæobotany is able to contribute towards the solution of developmental problems. The value of such work as this can hardly be overestimated; the evidence which is in this

<sup>1</sup> Williamson and Scott, p. 766.

<sup>2</sup> *Ibid.*, p. 769.

manner adduced rests on the best foundation, and must indubitably lead to a fuller recognition of the value of palæobotanical research as a factor of primary importance in phylogenetic inquiries.

In addition to the various points suggested in the description of these two extinct plants, and referred to in the foregoing summary, there are at least two reflections worthy of mention. In the first place, the work of many palæobotanists has clearly emphasised the need and importance of a more intimate acquaintance with the morphology of existing Cycads. Secondly, it would appear certain that among the numerous leaves of Palæozoic plants which it has been the general custom to regard as typical fern fronds, there must be some which belong to stems in which Cycadean characters more or less predominated. The probable connection of many "Cycadean" fronds with Bennettitean stems illustrates an analogous case among Mesozoic plants.

A word of the highest praise is due to Mr. Brebner for the admirable illustrations accompanying Williamson and Scott's memoir;<sup>1</sup> it would be difficult indeed to obtain more accurate and artistic reproductions of the almost incredible perfection of detail exhibited by sections of Carboniferous plants.

A. C. SEWARD.

<sup>1</sup> Williamson, W. C., and Scott, D. H. "Further observations on the Organisation of the Fossil Plants of the Coal-Measures." Part iii. *Lyginodendron* and *Heterangium*. *Phil. Trans. Royal Society*, vol. clxxxvi., B., pp. 703-729, pls. 18-29, 1896.





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## LIQUID CRYSTALS.

THE very name seems to be a self-contradiction. How can a liquid be a crystal, and how can a crystal be a liquid?

The term was introduced by Dr. Lehmann, of Karlsruhe, and relates to certain remarkable bodies which, if we accept his interpretation, must entirely revolutionise current views regarding the structure of solids and liquids.

In previous articles I have attempted to explain the newer theories of crystal structure, and have suggested that in their geometrical aspect they harmonise in a most satisfactory manner with observed facts. Now the very essence of these theories consists in the solidity of the crystal structure; it all the more behoves me, therefore, to call attention to the work of an investigator who regards these theories as of no essential importance and would deprive them of the basis on which they have been erected.

The observations of Lehmann are so curious and surprising that, whether his interpretation of the facts be correct or no, both the facts and the interpretation deserve serious attention. Although nearly six years have passed since the publication of his papers on the subject, little more than brief mention of them, so far as I am aware, has appeared in English; they have not been repeated either to be verified or invalidated; authors who have referred to them have been careful to quote the observer's own words, without either accepting or rejecting his conclusions; or, if they have expressed any criticism, have done so in an

extremely guarded manner ; and rightly so, for Lehmann is an acute observer and experimentalist who has contributed innumerable discoveries in the region of microscopical crystallography, and it was during the study of certain crystalline preparations by the microscopical methods of which he is a master that he encountered the remarkable phenomena which are the subject of the present article.

It was a botanist who, as in the case of so many interesting physico-chemical discoveries, contributed the initial observations. Dr. Reinitzer, of Prag, found that Benzoate of Cholesteryl had *two* melting-points, melting first at  $145^{\circ}$  to a dull and then at  $178^{\circ}$  to a clear liquid ; also (more curious still), that the former appeared to possess a certain double refraction. He forwarded the substance to Lehmann for microscopical study.

Shortly afterwards, Dr. L. Gattermann prepared samples of three other compounds—Azoxyphenol, Azoxyanisol and a substance having the composition  $\text{N}_2 \text{O}_3 (\text{C}_6 \text{H}_4)_2 \text{CH}_3 \text{C}_2 \text{H}_5$ —which behaved in a somewhat similar manner.

The crystals of Azoxyphenol, which we may take as illustrating the behaviour of all the three latter compounds, exhibit the following peculiarities. Warmed on a microscope slide they are suddenly transformed, at a temperature of  $134^{\circ}$ , into a substance which preserves the outline of the crystal, is strongly doubly-refractive, becomes dark four times when rotated on the microscope stage between crossed Nicols, and therefore behaves in all these respects like a true crystal. As is well known to all students of the subject, crystals differ from other substances in being anisotropic while they are homogeneous ; that is to say, all the properties of a crystal, while the same along parallel lines within it, are in general different in different directions. In the matter of their optical properties this character expresses itself in the double refraction exhibited by all crystals save those which belong to the cubic system ; and as a result of this birefringence, if the crystal be placed between two polarising Nicol prisms whose principal planes are at right angles, light is in general transmitted through the combination and is only extinguished four times as



the crystal is rotated through  $360^\circ$  on the microscope stage.

Azoxyphenol at  $134^\circ$ , therefore, behaves in these respects like a crystal, but, incredible as it may seem, is nevertheless a liquid; it does not retain a geometrical form, but is free to move in all directions.

If the preparation be still further warmed, it passes at  $165^\circ$  into a third modification which is also liquid, but not doubly refractive. It is possible to contrive that this molten substance shall contain small portions of the first, birefringent, liquid which float about in it as perfectly spherical drops.

Crystals of Azoxyanisol and the remaining substance resemble Azoxyphenol in their behaviour, the changes taking place at  $116^\circ$  and  $134^\circ$  with the former, and at  $87^\circ$  and  $140^\circ$  with the latter. The drops are regarded by Lehmann as really liquid crystals. It must be confessed that from his account of their appearance their optical characters do not seem to be precisely those of ordinary crystals, although, as we shall see, they do somewhat resemble those of warped or deformed crystals; the directions of extinction of one of the drops viewed through the crossed Nicol prisms constitute a series of radial and concentric lines corresponding in form to the equipotential curves in a spherical conductor which is traversed by an electric current entering at one end of a diameter and leaving at the other end. Viewed along the diameter, the drops present a black cross resembling that produced by sphæro-crystals or by material having a spherulitic structure.

Further, when viewed through one Nicol prism alone they are seen to be dichroic and to present different colours in adjacent quadrants. We have to do then at any rate with doubly refractive drops which possess a symmetrical disposition of their peculiar optical properties, and are unlike any other drops or any other liquid previously described.

In recent years many crystals apparently belonging to the cubic system have been found to be birefringent, and long and fierce has been the strife between those who have

offered explanations of their so-called optical anomalies. Some of these crystals when examined in thin sections in the polarising microscope are seen to possess a weak birefringence and to be partitioned into symmetrical areas, quadrants or sextants for example, in which the light may be extinguished uniformly over alternate areas successively as the crystal is rotated between the crossed Nicol prisms, and not over the whole section as in an ordinary crystal. Alum, Garnet and Boracite are familiar examples.

Other apparently cubic crystals which exhibit optical anomalies present the regular features of uniaxial and biaxial crystals belonging to other systems, the orientation of the optic axis, or of the optic axes, being different in the adjacent symmetrical partitions.

Neumann, Klocke, Klein and others have attributed the birefringence to strains set up either during crystallisation or during fall of temperature and resulting contraction after they have solidified; Mallard on the other hand propounded the theory that such crystals are pseudosymmetrical and consist of a number of uniaxial or biaxial individuals possessing less than cubic symmetry, twinned together so as to simulate the symmetry of the cube.

Both processes are illustrated by certain well-known examples. There are without doubt crystals belonging to the orthorhombic or monosymmetric systems which do aggregate themselves by twinning and constitute a complex crystal of apparently higher symmetry than their own, and it is equally true that birefringence may be produced by pressure both in cubic crystals and in uncrystalline substances; it is even possible to make gelatine moulds in the form of crystals, or of other geometrical solids, which perfectly simulate the optical characters of a uniaxial or biaxial crystal, and when examined in convergent polarised light show the familiar coloured circles or lemniscates characteristic of a crystal.

Lehmann, however, dismisses the possibility of his liquid crystals being merely very soft solid bodies, whose birefringence is produced by one or other of these causes or by the inclusion of some impurity, on the following



grounds: one of his drops suspended in a liquid of a density equal to its own assumes the form of a perfect sphere, like Plateau's drops of oil in a mixture of alcohol and water, and this would be impossible if the action of the surface tension called into play any opposing elastic force. He concludes that the particles of the drops are free to move as in a true liquid.

In the course of his numerous microscopic observations Lehmann has adduced many examples of crystals which have been mechanically deformed and continue to grow with bent faces and curved outline. He argues that a crystal does not cease to be one when it is bent; and that the extent to which it will recover its original form when the tension is removed depends merely upon the elasticity of the substance and not upon any essential difference between crystallised and uncrystallised material.

"According to current views," he says, "the crystalline condition consists herein, that the molecules are arranged in a regular order in which they are retained more or less rigidly by the elastic forces. Under certain conditions the system can be disturbed by heat, pressure, etc.; it then passes suddenly by virtue of local pressure into a new system which is more stable under the altered conditions, just as a half-opened pocket knife closes with a snap." Against this view he enters a forcible protest.

It is true that many crystals do behave in this manner; the researches of Mallard and of Lehmann himself have disclosed numerous instances in which a crystal when heated passes suddenly from one solid modification to another without any transition through the liquid condition. Nothing can be more startling than the behaviour of such crystals when seen for the first time.

A section of Boracite viewed in the polarising microscope is seen to be traversed by a number of doubly refracting lamellæ; but when the section is warmed to a temperature of  $265^{\circ}$  a cloud seems to pass suddenly over the crystal, which becomes quite dark; as the section cools twin lamellæ suddenly make their appearance again at the same temperature.

Again, to take another example, Pope has recently described the behaviour of Chloral Hydrate which, when melted on a microscope slide and allowed to cool, solidifies as a thin crystalline film consisting of needles of a uniaxial substance; if this be allowed to stand, biaxial plates begin to make their appearance among the needles and continue to grow until the latter entirely disappear, the uniaxial being entirely converted into the biaxial modification.

But between such substances and the liquid drops of Gattermann's preparations the difference is great. Something like a transition between the two is supplied by the Benzoate of Cholesteryl discovered by Reinitzer and studied by Lehmann in 1889, shortly before the other three yet more remarkable compounds came under his notice.

When the benzoate is warmed to  $178.5^{\circ}$  it melts to a clear liquid, and if this be allowed to cool slowly it becomes transformed into a dull white aggregate; at  $145^{\circ}$  true crystals make their appearance in this and continue to grow rapidly at the expense of the white mass, but when warmed they are again converted into the white substance. The granules of which the latter consists can be conveniently examined if the temperature be maintained at  $178^{\circ}$ , and though not absolutely liquid are found to be so plastic that they can be moulded and made to run into each other.

Lehmann's interpretation of these bodies was called in question by Quincke (6), who suggested that their behaviour was due to the presence of oil; but Lehmann has repeated the experiments with extra precautions and has further described the still more remarkable features of soft crystals of potassium oleate, which orientate themselves, come together in parallel positions and unite to form a single crystal.

Ordinary crystals are solids which can be deformed up to a certain point without any permanent change being produced in their form; they may, for instance, be bent by pressure and then return to their original form when the pressure is removed; unless the limit of elasticity has been passed, when they are permanently deformed or broken.



Now Lehmann has found that in many crystals the limit of elasticity is so low that without actual disruption they may by the application of very slight force be made to flow like shellac or certain other amorphous substances. He has long expressed his opinion that the essential feature of a crystalline structure is not, as is commonly supposed, the regular arrangement of particles which are held together by elastic forces to form a more or less rigid structure. If this were the case, he argues, a sufficient deformation would destroy the structure and reduce the crystal to the amorphous condition, and this has never yet been effected.

He inquires, therefore, whether the limit of elasticity may not in certain crystals be not only extremely small, as in the soft substances previously described by him, but actually zero, so that the material may be liquid and yet crystalline. If a liquid exhibits polarisation phenomena similar to those of a deformed crystal, is there any reason, he asks, why we should not regard it as a liquid crystal? In a bent crystal the optic axes and the directions of extinction are no longer straight lines but curves, and the birefringence is possibly to be attributed not to the relative arrangement of the particles but to their anisotropic nature. According to this view, the fusion of a crystal is simply its conversion into a fresh crystalline modification in which the limit of elasticity is zero, so that the substance behaves as a liquid; if the molten crystal is devoid of birefringence it may be that it represents a modification belonging to the cubic system.

It is suggested that the soft crystals prepared by Dr. Reinitzer and the liquid globules of Dr. Gattermann's compounds are crystalline liquids which possess a very strong double refraction. Reference must be made to the original memoir of Lehmann for a full account of the remarkable manner in which the liquid drops behave. His figures represent the normal drops viewed in the polarising microscope, when each resembles a globe with its meridians of longitude and its parallels of latitude marked upon it; the axis appears to resemble in some degree the optic axis of a uniaxial crystal. The spheres might be sup-

posed to consist of birefringent uniaxial particles arranged with their axes along the meridians ; during its formation, since any elastic force which might act in opposition to the surface tension is lacking, the particles would flow from one part to another in such a way as to make the surface potential energy a minimum, and the crystal would, like a drop of amorphous liquid matter, assume the form of a sphere. In the ordinary solid crystal the surface tension is different for different faces, and the crystal assumes a polyhedral form. The figures which accompany the memoir also illustrate the curious manner in which the drops may be deformed and broken up by squashing them between the slide and a cover glass. A globule may be broken up into two identical globules in this way ; two distinct globules may even be brought into contact and merged together so as to constitute a single globule.

The question next arises whether the isotropic liquid into which the liquid crystals are converted by further heating is also a crystalline liquid belonging to the cubic system, in which case the transformation of the drops to the isotropic liquid is merely a passage of a liquid from one crystalline modification to another, analogous to the passage of the birefringent lamellæ of boracite to the solid cubic modification when a crystal is heated to  $265^{\circ}$ . Now it is found that when boracite and similar substances are transformed into allotropic modifications the new crystals are regularly orientated with regard to the old. In the same way when the liquid crystals are transformed into the isotropic liquid by rise of temperature, and back again to the birefringent drops by fall of temperature, the latter preserve their original orientation. It is as though the terrestrial globes which they resemble had been fused into a liquid mass, and on separating again from this on cooling, solidify with their axes pointing the same way as before.

Hence, it is argued, the isotropic liquid may be only a new crystalline modification of the liquid crystals, and that, just as is the case in the transformation of solid crystals, the one modification may be converted into the other



without loss of orientation in the particles. In other words, in answer to the question with which we started, it is suggested both that crystals may be liquid, and that liquids may be crystalline.

It is scarcely necessary here to follow the author through the remainder of his inquiry ; let it be sufficient to mention that the three sorts of liquid crystals behave like isomorphous substances and mix together in all proportions ; that they always separate as pure drops from the liquid into which they can be converted by heating, and do not possess the power of dissolving substances which are soluble in the latter.

It will now be clear that Lehmann's definition of a crystal is no longer the current one. The regular arrangement of its particles into a homogeneous anisotropic solid is not an essential but an accident which may occur under certain favourable conditions.

The essential characteristic of a crystal is, according to his view, the power of growing in a supersaturated solution which is possessed by all crystals but not by colloids. Some liquids also may be crystalline, others may be colloids, the majority are probably the latter.

If I may venture on a word of criticism I would urge that here we are concerned partly with a question of words. It will be wise to retain the names crystal and crystalline in their old significations, rather than to extend them so as to include the birefringent liquids whose existence has been established by Lehmann. It may be that these remarkable drops are examples of liquid matter in which particles while free to move are compelled to preserve the same orientation, and differ in this respect from ordinary liquids. But whether this peculiarity of structure, whatever may be its nature, is really analogous to that of solid crystals is a question in which it will be better not to commit ourselves to an answer by applying the same name to both until more is known about the structure both of liquids and solids.

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H. A. MIERS.



## SUGAR: THE OUTLOOK IN THE COLONIES.

PERHAPS one of the most striking phenomena connected with the food of nations is the rapid increase in recent years of the consumption of sugar.

*Between seven and eight million tons* are used in various ways every year. When it is remembered that sugar is not usually regarded as a necessary food, but is rather classed as a "spice" to render other food palatable; and, further, that we have no means of judging the vast quantities used in China and India, and have accordingly not included them in our estimate, these figures appear to be well worthy of note.

The proportional quantities, again, in which this vast mass is shared by the different nations is a matter of considerable interest. The English-speaking races are the great sugar eaters. The average consumption of Great Britain and Ireland is 86·09 lbs. of sugar per head per annum; in the United States the proportion is 62·6 lbs. per head, while in France and Germany the figures are 30·61 and 26·78 respectively. This is all the more surprising when we consider that Germany at the present moment produces nearly double the amount of any other country, while France is an acknowledged rival in export.

This apparent anomaly is due to the curiously tangled state of affairs brought about by the "Kriegsprämien," the "war bounties". In France and Germany sugar is still a luxury—a spice—whereas it is becoming daily a more necessary article of Anglo-Saxon food.

The present condition of the sugar industry is thus peculiarly a matter of British interest. And, when it is broadly stated that most of the British Colonies engaged in growing the sugar-cane appear to be on the verge of bankruptcy, the interest becomes acute. The depressed condition in these Colonies may be traced to various causes, chief among which are (1) the competition of

European-grown beet, and (2) the various diseases at present attacking the canes. In the present paper it is proposed to deal more especially with the first of these.

Let us consider, at the outset, our national position regarding sugar. The British Isles consumed, in the year 1700, 10,000 tons of sugar; this amount had increased in 1800 to 150,000 tons, while the present consumption is 1,566,000 tons. Why has sugar taken such a hold on the people's fancy?

In Germany and France the quantity used is restricted by taxation, but in Britain sugar has a free market. This, in the main, explains the preponderance of British consumption. All races eat sugar if they can get it; and it is becoming more certain every day that this preference is due to the fact that sugar is a valuable muscle-making food.

It is perhaps worth while to dwell somewhat upon this point, for, although a matter of common enough observation in the Tropics, the facts are perhaps hardly appreciated among Europeans.

A striking example of the effect produced by sugar upon the human system may be seen among the labourers on West Indian sugar estates. There is a very evident improvement in the appearance and health, and, above all, the muscular strength of the negroes as the reaping of the crop proceeds. During this time they simply *live* upon the sugar-cane and its expressed juices. A doctor named Moseley, writing in the old slave days, noticed the same thing, and thus states the case in language more forcible than elegant:—

“In the West Indies the negro children, from crude vegetable diet, are much afflicted with worms. In crop time when the canes are ripe these children are always sucking them. Give a negro infant a piece of sugar-cane to suck and the impoverished milk of his mother is tasteless to him. This salubrious luxury soon changes his appearance. Worms are discharged, his enlarged belly and joints diminish, his emaciated limbs increase, and if the canes were always ripe he would never be diseased. I



have often seen old, scabby, wasted negroes crawl from the hot-houses apparently half dead in crop time, and by sucking canes all day long they would soon become strong, fat and sleeky.”<sup>1</sup>

Edwards in his history of the West Indies observes that “the time of crop in the sugar islands is the season of gladness and festivity to man and beast. So palatable and salutary is the juice of the cane that every individual of the animal creation drinking freely of it derives health and vigour from its use. The meagre and sickly among the negroes exhibit a surprising alteration in a few weeks after the mill is set in action. The labouring horses, oxen and mules, though almost constantly at work during this season, yet, when indulged with plenty of green tops of this noble plant, and some of the scummings from the boiling house, improve more than at any period of the year; even the pigs and the poultry fatten on the refuse.”<sup>2</sup>

It may be objected that the raw juice of the sugar-cane is very different from prepared sugar, and this is perfectly correct. While the sugar-cane may be advantageously eaten as a fruit, quantities of raw sugar are not likely to prove so wholesome. On the other hand it has been demonstrated that, at the moment of muscular action, grape sugar is fed to the muscle cells by the blood and oxidised.<sup>2</sup>

A practical test of the value of sugar as a muscle maker has lately been supplied by Dr. Vaughan Harley, who gives his results in a paper read before the Royal Society.<sup>3</sup> Dr. Harley’s experiments were conducted upon himself with Mosso’s “ergograph,” and great care seems to have been taken to obtain accurate results. He first of all determined the value of sugar when taken alone in the production of muscular work, and, on a fasting day, increased his capacity for work by 61 to 76 per cent. He next proved that the addition of sugar to normal diet had a marked effect in retarding fatigue. Seven ounces of

<sup>1</sup> Lunan.

<sup>2</sup> Chauveau and Kaufmann.

<sup>3</sup> Vaughan Harley.

sugar added to a small meal, increased the work done by his right and left hands 39 and 6 per cent. respectively, while after a heavy meal increments of 8 per cent. and 16 per cent. were registered. Lastly, by taking 250 grams ( $8\frac{3}{4}$  oz.) of sugar in addition to the ordinary diet, the work of an eight hours' day was increased 22 to 36 per cent.

We have no reason then to be ashamed of our national liking for sugar. The outcry regarding its injuriousness to the teeth is not often heard now ; and one is tempted, with old Lunan, to suggest that the marked preference of children for sweet things may very probably be one of those curious instincts which lead animals to choose their proper food.

It is interesting in view of these facts, to speculate upon the connection between our national sugar bill and the British taste for sports and violent exertion, so little relished or almost unknown among continental nations. We read that the American Indians, when making a difficult journey, used to provide themselves with a mixture of maple sugar and Indian corn, in the form of pressed cakes, half meal, half sugar. The well-known antiseptic properties of the sugar kept the food fresh, and a few spoonfuls of the mixture in half a pint of water formed a "pleasant and strengthening meal".

The following plants produce the sugar of commerce—the sugar-cane (*Saccharum officinarum*), the beetroot (a variety of *Beta maritima*), the sugar maple (*Acer saccharinum*) and certain tropical palms. Of these the two former are vastly more important and will alone be considered.

The division of commercial sugar into that obtained from the beetroot and that produced by the sugar-cane is a natural one. The two plants belong to very different orders, and the sugar is contained in different regions of the plant body. The processes by which the sugar is extracted are frequently dissimilar. The plants are denizens respectively of temperate and tropical climates, and are therefore produced under widely divergent conditions. It



thus becomes an easy matter to state the proportional quantities derived from these two sources for the world's market.

The following appears to be the approximate yield of sugar during the last two years, leaving China and India out of consideration as countries which do not export and concerning whose home consumption we have no data:—

		1894-5.	1895-6.
Beet,	- -	4,792,530 tons	4,323,899 tons
Cane,	- -	3,387,461 tons	2,652,000 tons
		<hr/>	<hr/>
Total,	- -	8,179,991 tons	6,975,899 tons

(The Cuban War, together with a diminished beet crop, accounted for the fall of over 1,000,000 tons in yield. The consumption was normal.)

It is clear that the world's market is already in the hands of the European beet producers; and it is most probable that during the next year or two the production of beet will be considerably increased, while there seems to be small hope of the extension of cane-growing because of the maimed condition of Cuba, the principal contributor.

The beetroot as a sugar-producing plant has a comparatively recent history, whereas the sugar-cane has been cultivated from time immemorial. The rapid increase of the beet industry may be gauged by the following facts. In 1747 Andreas Sigismund Marggraf, a professor in Berlin, made the important discovery that the sugars in beetroots, carrots and other fleshy roots of temperate countries were chemically identical with one another and with that of the sugar-cane; the sugar of ripe fruits, such as the grape, and that in honey being placed in a different class. This discovery did not however bear immediate fruit, and the first beet factory was not erected till 1801, near Breslau, in Silesia.

From the imperfect nature of the processes of extraction, and the great difficulty in eliminating the impurities from beet juice, it is more than likely that the enterprise would have died in its infancy. At this point, however, as has so

frequently been the case with beet sugar, a powerful impulse was received from the political condition of Europe. There appears to be no doubt that the introduction of beet factories into France by Napoleon I. was intended as a blow to the British Empire through her Colonies. England had attained her greatness through her Colonies, and Napoleon was determined to destroy them. The Continental ports were therefore closed to free British sugar; the price rose rapidly, and, under this artificial political protection, factories sprang up in various parts of France and Germany. Most of these collapsed, however, at the downfall of the Emperor.

We do not again hear much of beet-growing till about 1840. The British West Indies had just received their first serious rebuff in the emancipation of slaves, and it is quite probable that by this means the cultivation of the beet again received a political stimulus. From this time onward, the manufacture of sugar in Europe steadily and rapidly increased. The advance was and is artificial, in that payments are made on the Continent either directly or indirectly on all exported sugar; on the other hand, the British market, formerly a Colonial monopoly, has been opened more and more widely to the world's supply, first by the abolition of differential duties in favour of the Colonies, and later by the placing of sugar on the free list.

The British sugar-growing Colonies, being denied the protection they formerly received, have therefore steadily lost ground. The imports of sugar into the United Kingdom have increased five times during the last fifty years, whilst that received from the Colonies has diminished. This is partly due, of course, to their finding other nearer markets (the United States for West Indian Colonies and India for Mauritius), but the total production of the British possessions will not at present meet the home demand.

The accompanying table will illustrate the growth of British imports during the last fifty years, the gradual decrease of sugar received from the Colonies and its almost entire replacement by European beet:—



	1845.	1865.	1895.
Total Imports,	6,000,000 cwts.	11,000,000 cwts.	31,000,000 cwts.
From British Colo- nies (Cane),	5,000,000 cwts.	5,000,000 cwts.	3,000,000 cwts.
From Europe (Beet),	4,000 cwts.	300,000 cwts.	23,000,000 cwts.
From Germany alone,	—	30,000 cwts.	17,000,000 cwts.

Great Britain offers the only free market in the world. The great sugar-producing countries of Europe offer bounties on production or export, but find the funds for this by taxing the home consumption. An enormous agricultural and manufacturing industry is kept going by these at the cost of an enormous national burden. This burden is fast becoming unendurable, while, on the other hand, the privileged class of bounty-fed agriculturists is becoming more powerful a factor in the State. The net result for Great Britain is cheap and plentiful home sugar and the collapse of the sugar Colonies.

It is obvious that all this has an important bearing on the fact already alluded to, that we, in these small islands, are enabled to appropriate, as we do, nearly half the European consumption and nearly a quarter of the world's supply. In the agitation now on foot for the salvation of the sugar Colonies, the economic soundness of a protectionist policy is much to the fore.<sup>1</sup> The question is complex and many-sided, but one of the best rejoinders which free traders can make is a reference to the past effect of taxation upon consumption.

From 1800 to 1845 the British demand for sugar hardly kept pace with the increase of the population. The average consumption during this period was about 18 lbs. per head per annum, but in 1845 it had sunk to 17 lbs. At this latter date the import duty was reduced, and in four years the consumption increased nearly 50 per cent. "The

<sup>1</sup> *St. James's Gazette.*

protectionists maintained that the reduction of the duties would bring about no perceptible increase in the consumption of sugar. Lord George Bentinck, the champion of the sugar monopolists, went to the length of showing that under no conceivable circumstances could the people consume more than 5,600,000 cwts. of sugar in the course of a year. In the third year after the prophecy was issued the total consumption rose to considerably over that figure.”<sup>1</sup> In 1854 the consumption had exactly doubled its former figure, reaching 34 lbs. per head per annum. In this year the duties were increased again because of the Crimean War, and the consumption dropped from 34 to 28 lbs. From the close of the Russian war to the present time, finally, the consumption has steadily increased, reaching as already mentioned 86 lbs. *per capita* in 1895.

We have seen the effect of the Continental system of premiums upon the Colonial produce, and there seems little hope of improvement in the Colonies until the bounties are abolished. What likelihood is there of the latter taking place? The competing Continental nations are feeling the pressure of sugar taxation severely. Of these the principal producers are :—

Germany,	1894-5,	-	-	1,844,586 tons.
Austria,	„	-	-	1,055,321 tons.
France,	„	-	-	792,511 tons.
Russia,	„	-	-	615,058 tons.
Belgium,	„	-	-	243,957 tons.
Other Countries,	„	-	-	240,597 tons.

Various attempts have been made to arrive at an international understanding with the object of abolishing the bounties, as it is felt that the position is abnormal in that the industry is no longer such a one as needs artificial fostering. Obviously such action must be agreed upon by the larger exporting countries—Germany, France, Austria, Belgium and Holland. At the London Conference (1887) the British Government took the initiative in this direction,

<sup>1</sup> Reed.



but without result. In 1895 Austria and Germany opened negotiations without success. France alone refused to do away with the sugar bounties.

On the 30th of May of the present year, finally, a new Act was promulgated by Germany on the bounty question, to last till 1903. This is avowedly a warlike Act to compel France to agree to the abolition of premiums. As at first drafted, these were to be raised from 1·25 to 4 mks. per 100 kilos. on raw sugar, and from 2 to 5·25 mks. on refined. The adopted rates are, however, 2·50 mks. on raw and 3·55 on refined sugar; and the question is naturally mooted as to whether the original intention is still maintained. Is it a warlike move to render the continuation of the bounty system impossible—the burden devolving upon the taxpayers is supposed to be much greater in France than in Germany, the yield is lower, labour is dearer and there are fewer people to bear the load—or is it yet another concession to the powerful agricultural class, making the towns pay for agricultural depression?

The result of this legislation it need hardly be said is being watched with breathless interest. Austria has immediately followed suit: has indeed made a larger increase in her bounties. Holland is concerting measures. All eyes are fixed on France. What will be the next move in this bitter bounty war?

It will be readily seen that, while the cane-producing countries of the tropics were formerly in straitened circumstances, the effect of this new legislation is disastrous—the price of sugar being, as far as gold countries are concerned, below the cost of production. The British Colonies may be ruled out, as far as export is concerned, and, when it is remembered that some of these Colonies have all their eggs in one basket—growing nothing but the sugar-cane from one end to the other—and, further, that in their long struggle they have either locked up all their available capital in costly machinery, or are heavily mortgaged, it becomes a question of imperial policy whether the powerful and wealthy mother country cannot with advantage lend a helping hand to her struggling depen-

dencies. Otherwise, unless the "war bounties" cease, inevitable ruin stares these Colonies in the face.

In the presence of this great economic problem, all other considerations are placed in the background. The future seems only too clearly defined, although there may be temporary relief because of the state of affairs in Cuba, by whose war close upon 1,000,000 tons a year are withdrawn from the markets of the world.

There are other circumstances handicapping the cane-growing countries for which the beet growers are not responsible. The machinery on many of the estates is of a very inferior character indeed, and the amount of money sunk in this old machinery makes it very difficult for the impoverished owners to replace it by new. The method of extraction is therefore very inferior, and stands little chance of improvement. This matter of methods has always been held in the forefront by beet growers, because of the much greater difficulty in obtaining a pure sugar from their plant than from the cane; and the successive stages by which the beet plant itself has been improved in its saccharine content, and the processes of extraction and purification have been perfected, are well worthy of study, forming, as they do, a signal triumph in applied botany and chemistry. Suffice it to say that while in 1836 eighteen parts of roots were necessary to produce one of sugar, this quantity was reduced to 13·8 parts in 1850, 12·7 in 1860 and 9·25 parts in 1887.

Lulled into a false security, the cane growers have been content meanwhile to retain the same machinery by which a large proportion of available sugar has been passed to the refuse heap; and now that more economical working is necessary, circumstances render it difficult for them to extricate themselves from their false position. The time appears to have arrived when bankruptcy will clear away these cumberers of the earth and make room for others more ready to take advantage of the lessons which science is teaching them.



The fruits of adversity are bitter, but salutary, and great strides have undoubtedly been made in many places in the improvement of machinery as the successive blows have fallen upon the Colonies—first, the abolition of slavery, then the abolition of differential duties, and with these the monopoly of the British market, and lastly, and more crushing still, the unfair competition of bounty-fed beet.

If these bounties are abolished, the future of the sugar industry will doubtless be as full of surprises as the past has been. A renewed and more extended conflict will take place before cane and beet find their respective markets. It may be safely surmised that in Europe the removal of restrictions upon home consumption would vastly increase the quantity required—it would probably be largely increased in France, and is even now steadily increasing in Germany. In Britain numerous industries would be affected, prominent among which would be the decayed refining industry and the greatly developed jam trade. And, sobered by sad experience, the Colonies would take up the question so long neglected of bettering their extracting processes, and new machinery on economical lines would lay the foundation to a future of profitable industry.

But the planters would also have to devote increased attention to the improvement of their canes—not only as regards their saccharine content, but also with regard to their capacity for resisting disease. There are, in fact, at the present moment, diseases in the cane fields which threaten to sweep away some of the most magnificent varieties of the sugar-cane.

There are many scientific questions of great interest connected with the origin and spread of these diseases, and it is proposed in a future paper to deal with these, and pass under review the strenuous efforts being made by scientific men in the tropics both to produce improved varieties of the sugar-cane and to combat their diseases.

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C. A. BARBER.



## THE CELL AND SOME OF ITS CONSTITUENT STRUCTURES.<sup>1</sup>

FROM old time it has been one of the highest aims of Philosophy to penetrate the veil which obscures the mysteries of life and of organisation, and the concentration of such an immense amount of attention on the minute details of cell structure during the past few years is the outcome of a conviction that this is one of the most favourable means of attacking the problems we seek to solve. But so vast a mass of knowledge has been acquired that perhaps we run some danger of missing the goal amid the maze of paths which have been opened up towards it. And thus it may not be altogether amiss to stand still for awhile and try to take stock of our position, to criticise the various conflicting opinions, and to test as far as may be, the foundations on which they rest. And one of the first facts to which it is necessary to be warily alive, in inquiries such as these, is that the vast majority of the observations on which we rely have been made on the dead cell. That is, we are trying to form a conception of what goes on in *living protoplasm* from results gained by a study of structures preserved in a dead substance which is certainly no longer protoplasm. We assume, but we ought to be constantly testing the validity of our assumption, that in what we call well-fixed material, at any rate the grosser structural arrangements of the protoplasm as it existed in the living condition are preserved to us. But the difficulty lies exactly in determining our criterion of proper fixation, and a neglect of this precaution may render utterly valueless even an accurate description of what an observer sees, unless he can satisfy his readers that he is not, as a matter of fact, merely describing artefacts, appearances artificially produced during the process of killing. Indeed, one often hears this *a priori* objection urged against cytological work

<sup>1</sup> Read before a combined meeting of Sections D and K of the British Association, 22nd September, 1896.

in general, and I think I may safely say that no one who has had much experience in actually watching the effect of reagents on the living cell will be inclined to under-estimate its importance.

I am not now speaking of those obvious contractions and distortions, the well-known results of defective treatment of the material at some stage between killing the protoplasm and finally observing its structure with the aid of the microscope. I am thinking rather of the insidious effects of certain reagents which, in some cells and tissues at any rate, are able to evoke *post-mortem* changes so definite in their character that only careful and wide comparison enables one to set them down as undoubtedly artificial. It may be the reagent was too much, or too little, concentrated, or that it happened to be unsuitable for some reason or another to the particular tissues under investigation.

But there are other perils, of a more general, and perhaps one may say of a more subjective, nature, to which the student of cytology is specially liable. I refer in particular to that one of over-generalisation. The fact is, the subject is so essentially a study of an enormous number of minute details, the relative importance of which is still for the most part uncertain, that one is more than usually exposed to the danger of drawing too wide conclusions from too narrow an area of fact. That this is a real and not a fanciful charge, a slight acquaintance with the first-hand literature of the subject is enough to prove; elaborate general theories are based on the study of, it may be, a particular set of nuclei belonging to a single organism. The time so spent would have been better employed in extending the authors' range of vision over other groups of the animal and vegetable kingdom.

The phenomena which are successively exhibited during the processes resulting in the formation of the reproductive cells in *Ascaris megalocephala*, for example, and in their fusion during the act of fertilisation, are so striking that it is small wonder that they have been, and by some people seem still to be, regarded as representing a general type to which other organisms ought to conform, at least in the



broader outlines. Nevertheless, we know, as a matter of fact, that *Ascaris* will *not* serve as a general type ; we know that differences exist between it and many other organisms in almost every detail, and that only the final result is the same. It is obvious, then, that clearness of differentiation alone will not serve as a criterion of fundamental importance in the case of any given structure, and, perhaps, put in this bald way nobody would expect it would. I have mentioned *Ascaris*, because it has come to be a familiar object to many people—all the principal phenomena of its nuclear division and of fertilisation can readily be seen without employing any of the more refined methods of technique. But I might equally well have taken the Salamander, which has served as the chief object of Flemming's epoch-making researches, and I may the more specially mention the Salamander in this place, since it differs in so very many details from *Ascaris*.

Having cleared the way thus far, I now propose to consider some of what we may perhaps regard as the chief groups of phenomena associated with nuclear division which are known at the present time. In this way I believe we shall be best able not only to estimate the relative importance of the several structures involved, and to understand their mutual interaction during the process of karyokinesis, but we shall further have acquired a material basis from which to criticise the views now current as to the way in which the fact of heredity is to be harmonised with the complex processes proceeding within the cells themselves.

For it is to the nucleus and the protoplasm that we must turn for the essential factors which determine the structure and govern the organisation of living beings. But we meet with differences of opinion at the very threshold of our inquiry, as to the share allotted to the nucleus and to the cytoplasm respectively in initiating the process. Some say the stimulus comes from the protoplasm, some say it comes from the nucleus, a third party ascribes it to that veritable *Deux ex machina* the centrosome ; and Boveri, if I understand him rightly, postulates yet another organ, a specialised mass of protoplasm in the vicinity of the centrosome, which

he calls the archoplasm. Of all the so-called organs of the cell, none has been more vigorously investigated with so little agreement in general result as the centrosome, or centrosphere. In fact, when one dips into the bulky literature which has grown up around this body, the dimensions of which sometimes border on, and often dip below, the visible, one is filled with admiration at the vastness of the labour, and with sorrow at the utterly incommensurate result. Perhaps the great interest attaching to it is to be largely attributed to the clearness with which it presented itself to Van Beneden in *Ascaris*,<sup>1</sup> in which animal its importance was first insisted on. In many other animal cells it is also clearly seen, and I may say that in another invertebrate animal I have, thanks to the kindness of Professor Rückert in Munich, seen centrosomes almost surpassing those of *Ascaris* itself. But, on the other hand, there are many other animals in which these structures appear under a simpler form. The dense aggregation of protoplasm is not observed in a number of cases even at the time most favourable for distinguishing it if present. Again, even in *Ascaris*, it would seem that it is not exactly a permanent *morphological* constituent of the cell; for Boveri and others had observed that it becomes indistinguishable at a later stage of nuclear division. Here, then, we must assume a "physiological" persistence, or use some other expression to save the individuality of the "cell organ". But is it really necessary to regard the centrosome as a universally essential structure at all? We know that, curiously enough, in the divisions which result in the cutting off of the polar bodies from the maturing ovum, it is very commonly and perhaps typically absent, and there is a large amount of positive evidence to show that with the single exception of *Myzostoma*, described by Wheeler,<sup>2</sup> and apparently well authenticated, it is entirely lacking from the

<sup>1</sup> E. van Beneden et Neyt, "Nouvelles recherches sur la fécondation et la division mitotique chez l'ascaride mégalocephale," *Bull. Ac. Roy. de Belgique*, 1887.

<sup>2</sup> "The behaviour of the centrosomes in the fertilised egg of *Myzostoma glabra*," Leuckart, *Jour. of Morph.*, vol. x.



mature ovum. Indeed, so generally is this opinion shared, that Boveri, one of the staunchest upholders of the importance of the centrosome, regards its importation by the spermatozoid during fertilisation as one of the necessary conditions of segmentation. But it is difficult to reconcile this assumption with the results of an investigation carried on by R. Hertwig<sup>1</sup> on Echinoderm eggs.

This writer, in the first place, agrees with all the recent observers who have investigated these objects ; that Fol was quite in error in attributing a centrosome to the egg. In fact, the whole history of the supposed fusion of centrosomes arising from the male and female cell respectively is one of the best object lessons I know of wherewith to enforce the remarks about methods which I prefaced to what I have to say to-day. But R. Hertwig discovered that, although the female cell contained no centrosome (that is, no "organ of division"), this circumstance did not prevent the nuclei of these unfertilised eggs, when they had been kept for a sufficiently long time, from starting through the first phases of karyokinesis ; and he incidentally made the interesting discovery that certain stimulants hurried up the process, so that, although normally it only begins after the eggs have been extruded about two days, under the influence of very dilute solution of strychnine it commences in about one and a half hours after extrusion. It is true that for the most part the division of the nucleus was not completed, but that does not affect our present argument ; the important point is that in the admitted absence of the so-called *division organ* the division itself could be initiated.

But Hertwig went further with his experiments. He found that by applying chloral to the spermatozooids and ova, before mixing them together, he was able to inhibit the *fusion* of the male and female nuclei, although the spermatozoid still retained the power of penetrating the egg sufficiently to become embedded within its protoplasm. When this occurred, spindles were formed, both in connection with the

<sup>1</sup> " Ueb. die Entwick, des unbefruchteten Secigeleies," *Festschr. f. Gegenbaur*, Bd. i., Leipzig, 1896.

male and female pronucleus, but both were completely independent of each other. This proved two things : first, that the male pronucleus was able to undergo division on its own account when within the egg protoplasm, as had already been shown in another way by Boveri ; and, secondly, that the stimulus,—whether arising in the first instance from the male nucleus alone, or as the result of the interaction of it with the surrounding protoplasm,—could be transmitted so as to set the other, the female nucleus, dividing. And there is another fact which seems to indicate that the division is, really, the result of the *mutual interaction between the nucleus and the cytoplasm*, namely, that a spermatozoid of *Echinus*, when introduced either into a ripe egg or into a non-nucleated fragment of such an egg, at once begins to divide, but that if introduced into a similar egg, or part of an egg, which is not ripe, no change whatever results. All these facts, I think, militate against the great importance claimed for the centrosome as an actual organ of division, and go to show that the *nucleus and cytoplasm as a whole* are the principals concerned in the process.

There is a good deal of uncertainty surrounding the individuality of the centrosome in plants. It corresponds to the centrosome in its original sense as used in animals, but perhaps not to the modern extension of it which has been invented to embrace those highly inconvenient structures described as microcentra by Heidenhein<sup>1</sup> and others. Sometimes the centrosome is marked off from the surrounding radiations by a clear space, and in this case the resulting sphere is termed the centrosphere. Now, it is probably a significant fact that all the clearest demonstrations of centrospheres have hitherto been met with in the lower plants. In some Diatoms they are said to be so obvious as scarcely to require staining to render them visible. In *Sphacelaria*, originally described by Strasburger,<sup>2</sup> they are extremely

<sup>1</sup> M. Heidenhein, "D. Hautdrüsen, d. Amphibien," *Sitz. d. Würz. b., Phys. Med. Gesells.*, 1893 ; also, "Ueb. Bau. u. function d. Riesenzenellen im Knochenmark," *Würzburger Verhandl.*, 1894.

<sup>2</sup> Strasburger, *Schwarmsporen, Gameten, pfl. Spermat. u. d. Wesen d. Befrucht*, 1892.



clear during the actual stages of nuclear division. Whether they retain their identity during the actually resting condition seems to me to be doubtful. At any rate, it would require some confidence to discriminate them in the absence of all radiations, from the other granules which lie in the vicinity of the nucleus, each likewise surrounded by a clear sphere. In Liverworts again they are often extremely well defined, and at the same time they appear in such a peculiar fashion in many of these plants that I may perhaps be pardoned for drawing special attention to them here. It has not, so far, been found possible to detect with certainty the existence of centrosomes in the resting cells of these plants, but when nuclear division is about to take place, a minute but easily recognisable body is found at the spot from which the radiations are beginning to appear. During the successive bipartitions which go on in the young sporogenous tissue of such a liverwort as *e.g.* *Fossombronia*,<sup>1</sup> they are particularly plain at the earliest stages of karyokinesis. But when the spindle is complete and the chromosomes are forming the equatorial plate, the radiations die away at the poles and then a centrosome is no longer distinguishable. The same thing may be still more easily seen during the germination of the spores of *Pellia*, a very common Hepatic; and convenient, because the spores germinate while still within the sporogonium, and hence all stages may be found close together. But as the process of karyokinesis advances the radiations once more appear, and with them, the centrosphere usually again becomes visible. Is it possible that this temporary obliteration of the polar radiations is to be taken as the expression of a relatively stable, if transient, condition of equilibrium, and that, with the temporary cessation of movement in the protoplasm, the differentiation of the centrosphere and the attendant radiations are for the time being in abeyance?

Perhaps some one may object that, after all, I have as yet omitted to state the strongest evidence for the claims of

<sup>1</sup> Farmer, "Nuclear Division and Spore Formation in the Hepaticæ," *Annals of Botany*, vol. ix., 1895.

the centrosome to be regarded, generally speaking, as a permanent if often concealed "organ of the cell". I mean the wide-spread and apparently well-founded belief that it is not formed *de novo*, but only arises as the result of division of a pre-existing centrosome. I shall revert to this question later; but in this place will mention three sets of facts which are difficult to reconcile with the absolute continuity-of-existence theory. The first I take from the animal kingdom. Brauer<sup>1</sup> observed, whilst investigating the development of the parthenogenetic eggs of *Artemia salina*, that there was no centrosome associated with the first polar division, but that afterwards when the egg was ready to segment to form the embryo a centrosome became visible. Brauer, it is true, remarks that the centrosome might have existed in a modified or distributed state during the first karyokinesis; but this is merely a pious belief, and all more recent work, with the exception of Hacker's statements as regards *Ascaris*, seems to tell against it. Brauer himself only puts it forward apparently as a means of saving the reputation of his egg centrosome. The second and third sets of facts I shall draw from instances of which I have more special personal knowledge. In the liverworts, the two main subdivisions of Marchantiaceæ and Jungermanniaceæ are characterised by differences in the formation of their spores. The former, the Marchantiaceæ, do not for the most part call for special notice. With the exception of *Fegatella* and *Targionia* the divisions in their spore mother cells so far as is known coincide in their main features with those seen during the formation of dicotyledonous pollen grains. That is to say, the nucleus undergoes two perfectly normal bipartitions. The shape of the mother cells is commonly (with the exception of the two genera above mentioned) spherical. It is widely different in the Jungermanniaceæ.<sup>2</sup> Here the mother cell, as it grows prior to its final division, becomes a four-lobed body, and

<sup>1</sup> Brauer, "Zur Kenntnis d. parthenogenetisch sich entwickelnden Eies von *Artemia salina*," *Archiv für Mikr. Anat.*, Bd. xliii.

<sup>2</sup> Farmer, *loc. cit.*



the degree of the lobing varies in different species. The important fact for our purpose is that in all these four lobed cells, at the commencement of division, *four*, and not two, centrospheres appear simultaneously, placed symmetrically at the periphery of the nucleus. Further, in those spore mother cells in which the lobing is not very prominent, the four centrospheres ultimately coalesce in pairs, so that a normal bipolar spindle is the result as soon as the first division is completed, the daughter nuclei begin to divide in a perfectly normal, that is, bipolar, fashion. But in the cases of extreme lobing, as in *Pallavicinia*,<sup>1</sup> there is no room for a symmetrical bipolar spindle, and the four poles persist throughout the entire division. This is modified, inasmuch as two divisions of the chromosomes occur without an intervening period of rest, and thus the four daughter nuclei are formed simultaneously; transitional stages, however, connect the two extremes. The general conclusion impressed on the mind of the observer is, that it is the *shape of the cell* which in some way determines the proximate character of the division.

Now, these facts seem to me to militate strongly against the permanent organ—and individuality—hypothesis of the centrosome. How can one imagine that the centrosome could in these cases become divided into four, and direct the protoplasm to transmit each quarter to its right place, without betraying any evidence of the process? For it is hardly conceivable, that in a large mass of material, all fixed at the right time, such stages, if present, could have escaped observation when they were being directly searched for. To my own mind a more natural explanation seems to be that the centrosome in this case originated, *de novo*, at the spots at which they were found, and that their singular mode of distribution is to be regarded as the result of the relative degree of independence associated with the four masses of protoplasm, an independence due primarily to the greater or less complete severance of the living contents of any one lobe from those of the rest. And, furthermore, the

<sup>1</sup> *Annals of Botany*, vol. viii., p. 47 *et seq.*

otherwise astonishing differences observed between nearly allied plants are, on this hypothesis, no longer surprising.

It seems to me that a consideration of an exceptional case like the one just quoted, is especially useful in enabling us to form a judgment as to how far the whole process of cell division may be the result of physical forces operating in the cell, or how far we are justified in invoking the aid of a special organ of division to rescue us from intellectual uncertainty. It must be remembered that, if we have recourse to the centrosome as the prime operator in these matters, we practically give up attempts at arriving at a solution of the difficulties. For we are no nearer to comprehending the phenomena of cell division than we should be as regards the origin of protoplasm itself if we were to assume that it was brought here in the first instance on an aerolite. On the other hand, if we accept the view of Heidenhein that the centrosome is a mere insertion point of the forces set free in the protoplasm, its nature becomes a secondary matter, and we know, as a matter of fact, that its position may vary, it may be intranuclear during the spindle formation, as in the *univalens* variety of *Ascaris megalocephala*, or, on the other hand, it may be extranuclear, as in the other (*bivalens*) variety of the same animal. These questions as to position, however, lose their importance if we take this view of its *rôle* in karyokinesis. Furthermore, the disparity of size between the two centrosomes belonging to opposite ends of a dividing nucleus, which was pointed out amongst others by Reinke,<sup>1</sup> no longer astonishes us, nor does the fact that here and there spindle fibres seem occasionally to mistake an isolated granule for a centrosome, judging at least from the manner in which they diverge towards it. Still once more, the facts noticed by Belajeff<sup>2</sup> and others, that during the division of the pollen mother cells of certain flowering plants the spindle fibres are frequently at first *not* directed to two points, but only later converge thither, become less unintelligible; the directions of the strains have,

<sup>1</sup> Reinke, "Zellstudien," Theil II., *Archiv f. Mikr. Anat.*, Bd. xlix.

<sup>2</sup> Belajeff, "Zur Kenntniss d. Karyokinese b. d. Pflanzen," *Flora*, Erg.-Bd., 1894.



so to speak, not yet become focussed. Finally, the general radiation round the entire nucleus, figured by Guignard<sup>1</sup> and others in the pollen mother cells of *Lilium*, no longer surprises us, although, on the assumption of the existence of persistent centrosomes, whose supposed business it is to manage these matters, the phenomenon strikes one as odd.

Perhaps one might even go farther, and ask if the facts really warrant us in thinking that the centrosome is more than an indication of the position at which the forces are in equilibrium ; perhaps the centrosome is no more the *cause* of the forces than are the dead leaves and broken bits of wood in any way effective in producing an eddy, the centre of which they mark. The obvious objection that in many cells the centrosomes endure from one division to another by no means proves that they act, even here, as the directive agents in initiating and presiding over each mitosis. We know practically nothing as to the mechanical conditions of protoplasmic contractility ; but it may perhaps be pointed out that it is not necessary to suppose that the particles which we may for the moment assume to be coerced to form a centrosome, should disperse when in a medium of approximately the same density as themselves, even when the conditions which caused them to become aggregated, in the first instance, are no longer operating ; and, secondly, I may mention the fact that they are best seen in tissues in which cell division is active, and thus one scarcely need look for their dispersal during the short quiescent intervals. Finally, there is the microcentrum of Heidenhein, in which it would seem possible that such a scattering of the particles is actually taking place. The fact of their division in cases like that of the well-known Hermann's spindle<sup>2</sup> hardly helps the matter one way or another. It will be remembered that Hermann discovered that the spindle arose, in the Salamander, as a concomitant of the divarication of the centro-

<sup>1</sup> "Nouvelles Études sur la Fécondation," *An. Sci. Nat. (Bot.)*, 7<sup>e</sup> Série, t. xiv., 1891.

<sup>2</sup> For figures and description see O. Hertwig, *The Cell* (Eng. trans.), p. 185.

somes quite independently of the nucleus. Whether we suppose that forces are at work in the protoplasm which split the original centrosome and drive the two halves asunder, with the resulting formation of the so-called central spindle, or whether the *vis viva* originates in the centrosome itself, the appearances would be precisely the same, and, as a matter of fact, both views have been urged.

But if we allow that the centrosome owes its existence to the energy liberated in the protoplasm, this does not exclude the hypothesis that a periodical repetition of certain conditions might as often lead to the formation of a centrosome. Indeed, from what we already know of protoplasm, it is not difficult to imagine, should the presence of such a structure conduce to the more adequate accomplishment of karyokinesis, that it might probably be differentiated in this way. All the facts we possess on the subject of nuclear division go to show the existence of an almost infinite amount of variety in the details of the process, and any possible physical condition which facilitated its completion, or which enabled its course to be run through more smoothly, would probably come to be more or less closely realised. And the very belief that centrosomes *are* in some way useful, is founded on the frequency with which they occur, and on their relation with the spindle.

But however this may be, we can hardly escape the conviction, even on the independent-organ hypothesis, that it is the protoplasm which, after all, carries its "division organs" into those positions which determine the direction of division, a direction that is often, perhaps always, so exactly in accordance with what mathematical theory demands that its plane can be predicted from the contour of the cell. And in many of the apparent exceptions to this rule, as for example in the eggs rich in yolk, to be found in many animals, and perhaps also, though less clearly, in the oospheres of *Pinus*, the difficulty vanishes as soon as one realises that the protoplasm is not homogeneous throughout the whole cell, but is obviously of a different texture in one part, as compared with the rest.



Taking leave of the centrosome for the present, we may briefly glance at the structure and mode of origin of the spindle. And here, too, we are confronted by an astonishing amount of diversity in detail, accompanied by a surprising degree of similarity in the final result. The most complete form of spindle is that known as Hermann's spindle, to which I have already alluded. Here the primary fibres, which form a central strand, arise in the protoplasm and have in the first instance no direct reference to the nucleus at all; but, by-and-by, from the poles of this central spindle radiations extend through the rest of the cytoplasm, and are directed in special abundance to the nucleus. The chromosomes which are now in process of formation are roped up as it were on to the central spindle, finally becoming symmetrically arrayed around it. During the division of the chromosomes and the divarication of their respective halves to opposite poles the movement seems to be effected by a contraction of the peripheral roping spindle fibres, the central spindle merely serving as a kind of railroad along which the chromosomes travel.

There are, however, other instances in which the same thing is effected, but the mechanism is less complete. In the spore mother cells of *Fegatella*<sup>1</sup> the spindle is of a remarkable form, probably owing in part to the peculiarly compressed shape of the cell. The spindle is not formed in the same way as in the Salamander, but it originates simultaneously at two points not quite 180 degrees apart. Thus the chromosomes are at first grouped in an angle of the spindle. The point which is of interest to us just now is the fact that at the earliest stages there seem to be no fibres which run continuously from pole to pole; this condition is, however, speedily reached by the fusion of a number of fibres which meet half way between the two poles.<sup>2</sup> Then

<sup>1</sup> Farmer, "Further Investigations on Spore Formation in *Fegatella conica*," *Annals of Botany*, vol. ix.

<sup>2</sup> Drüner (*Jenaische Zeitschr. f. Naturw.*, Bd. xxix.) asserts that in the Salamander the central spindle begins as the result of a *fusion* of radiations, such as occurs in *Fegatella*. This is contradicted by Meves (*Archiv f. Mikr. Anat.*, Bd. xlviii., p. 19), who upholds the view that they are continuous from the moment at which the two centrosomes begin to divaricate.

the poles move farther apart, though whether owing to a *stress* in the now continuous axile strand or whether owing to the *strain* caused by the contraction of the peripheral fibres which run out to the cell wall, it is impossible to say. It suffices for present purpose that here, too, as in the Salamander, the triangular character disappears, and the chromosomes are pulled to the axile strand, on which they proceed to undergo division in the usual way. In other plants there is not such an obvious formation of a central core of fibres, but in reality it is probably of common occurrence, and a form of it can with certainty be distinguished in many cells; that is to say, some fibres may be seen to run right across from pole to pole, while others only run from the pole to the chromosomes. The final result is the chief thing, the actual method followed being subject to indefinite variety in detail, depending doubtless on the local conditions existing in the cell.

Again, the spindle, at any rate the part of it which lies between the two poles, may be entirely of nuclear origin, and it thus stands in sharp contrast with such a form as that existing in the Salamander. This kind of spindle occurs in *Ascaris meg.* var. *univalens*, in which the centrosomes are also intranuclear, also in the spermatogenic divisions in some birds, as was noticed by Moore a year ago. In plants it occurs in some fungi; in algæ Fairchild observed it in *Valonia*,<sup>1</sup> and it also occurs in *Fucus*. In the latter plant, indeed, it can readily be seen to arise within the nucleus, as the result of a differentiation of the achromatic substance, and the division of the chromosomes occurs while the original nuclear wall is still unbroken. This, to my mind, is strong evidence against the existence of any special spindle-forming substance, which is postulated by some writers. I believe the spindle to be nothing more than a differentiation in the pre-existing protoplasm, and I see no need to further complicate a matter already sufficiently bristling with difficulties by in-

<sup>1</sup> Fairchild, "Ein Beitr. z. Kenntniss d. Kernth. b. *Valonia utricularis*," *Ber. d. Deutsch. bot. gesell.*, xii.



roducing any hypothetical substance which by assimilation and growth shall produce the body in question. The rapid differentiation, the exact correspondence in position with mathematically determinable lines of force, and the gradual transition of the radiations themselves into the general protoplasmic structure of the cell as well as the apparent indifference as to its cytoplasmic or nuclear or even mixed origin, are to my mind strong arguments in support of the contention that we need not yet fall back on a special substance—a sort of amorphous organ, as the *fons et origo* of the spindle fibres. It is not a little remarkable, however, to observe how very positive many people still seem to be as to the correctness of looking exclusively to either a nuclear, or to a cytoplasmic, or to some *special* source for the material of which the fibres are made up.

As we have met with so much variety in the character of the cell structures we have hitherto considered, we might be prepared to find differences extending even to the chromosomes themselves. And as a matter of fact we do. It is of course impossible to enter into details here, the subject is much too extensive ; and I purpose only to mention those deviations which seem likely to cast some light on the obscurity which clothes the corporeal organisation which underlies, and perhaps is the cause of, what we term heredity.

It has become customary to regard the nucleus as the bearer of the hereditary qualities of the organism or of the cell, but the reasoning on which this view is based is not above reproach, for even in fertilisation a certain amount of cytoplasm is imported into the egg along with the male nucleus.

It is true that since the story of the fusion of male and female centrosomes during fertilisation seems to have become generally discredited, the interest attaching to the cytoplasm has again given way to comparative indifference in so far as questions of heredity are concerned ; and, indeed, what experimental evidence we have appears all to tell in favour of the importance of the nucleus. Boveri's beautiful experiments, in which he fertilised non-nucleated fragments of the

egg of one species of echinoderms with the spermatozooids of another species, are a striking case in point. Boveri has recently repeated these observations, with the same result as before—namely, that he was able by adding spermatozoa to non-nucleated portions of ripe eggs to raise pure larvæ which resembled the *male* parent in every case, while in control series he found that when hybrids were formed with *nucleated* portions of ova, the resulting larvæ exhibited characters *intermediate* between the two parents.

As from the standpoint of heredity the nuclear divisions which are associated with the reproductive cells are of special interest, I will ask you to consider a few typical cases. And in the first place, one of the most striking and most uniformly recurring features connected with these cells lies in the numerical reduction to *one-half* of the previous number of the chromosomes. This reduction may be immediately associated with the differentiation of the sexual cells themselves, as is the case in animals, or it may occur at some other period in the life-history of the organism. Thus in all the Archegoniate and Phanerogamic plants which have been investigated with this object in view, the reduction is manifested in the first division of the spore mother cell; and if, as in the embryosac (macrospore) formation of *Lilium*, development takes a short cut, the reduced number becomes necessarily shifted to a later period than usual, but it manifests itself at the earliest time after these suppressed divisions would otherwise have occurred. Thus, in *Lilium*, the halved number of the chromosomes appears in the first division of the embryosac, whilst in *Allium*, in which the embryosac mother cell divides once (not twice) before forming the embryosac, the reduced number is apparent at this earlier stage. In the pollen grains, or microspores, the reduction likewise appears in the first division of the pollen mother cells. But it is a noteworthy fact that in *Fucus* the reduction takes place at a stage precisely corresponding with that in an animal, and this marks an important difference between *Fucus* and the Archegoniate plants in which the process has hitherto been most thoroughly investigated. It appears to indicate that



*Fucus* is probably a long way removed from the main series of plants, an opinion already shared by many people on other grounds. Indeed, it seems tolerably clear that there is nothing of the nature of that alternation of generations in *Fucus* which is so eminently characteristic of the main plant-series.

A phenomenon of such general occurrence as this of reduction is obviously one of profound importance, and it is scarcely to be wondered at that the divisions which are concerned in effecting it should have formed the subject of very many investigations. It was, and is still, hoped that some definite evidence might be forthcoming as to the way in which hereditary characters are transmitted and new qualities arise. For it has been tacitly assumed by nearly every one who has written on this subject that the teleological explanation of the whole process is in some way bound up with that of heredity. The only positive and bare inference however is that since the male pronucleus contributes the same number of chromosomes as the female a numerical reduction is necessary at some period in each sexual cycle, unless the number of chromosomes is to increase in geometrical progression in every succeeding sexual generation.

But with the general admission that a reduction is effected, all agreement between various investigators ceases. There is hardly less difference in opinion as to the manner in which the process is actually brought about than as to the meaning of the various stages. And once more, when we take a general survey of the facts, I think we see that the same result may be accomplished in a variety of ways; hence at present it is perhaps premature to lay too much stress on the details of this or that set of observations (however accurate they may be for the particular subject of investigation), in endeavouring to frame general theories. And so, though theorising is very inviting in such a subject as this, I think I shall best serve the purposes of this discussion by bringing before you some of what I conceive to be the most salient points characteristic of the reduction divisions in plants and animals, only criticising those views

which have been advanced when there appears to be definite evidence opposed to them.

One of the most remarkable facts which confront one in connection with chromosome reduction is that *two* divisions should be almost invariably associated with the process. The only exceptions I can recall are those in which, as in Lily embryosacs, the mitoses in which it would have normally been accomplished have been telescoped into a shorter course, owing to the suppression of the divisions of an embryosac mother cell.

And the second point lies in the rapidity with which the two divisions follow on each other; the daughter nuclei resulting from the first mitosis rarely go into the complete resting stage before they commence to divide once more. And this perhaps helps us to understand how the process may be so compressed as to admit of the telescoping of one or both divisions, such as is seen in the Lily.

The third point of general importance is the very long period of rest and growth through which the nuclei pass just before entering on these divisions. In pollen mother cells, and in the sporogonia of liverworts for example, the final number of spore mother cells is reached tolerably early, and then a very long interval elapses before they rush through the final mitoses. The same thing, though in a somewhat less degree, is to be seen in the reproductive glands of animals.

Fourthly, when the nuclei are preparing for the important divisions, after their long period of growth, they go through several remarkable phases, which are common both to plants and animals. I have seen them in all the cases I have investigated or had the opportunity of examining. The cells become extremely sensitive to injurious substances, and it is to this cause that the well-known difficulty of killing and fixing properly is due. Moreover, the linen framework in which the chromatin is increasing in quantity becomes lumped together in a highly characteristic manner; this is a transient phenomenon, and most people have been inclined to regard it as due to imperfect fixation. But I have myself seen it in the living cell in some animals, and



the same phenomenon has been also observed in living pollen mother cells.<sup>1</sup> But whether the appearance is connected with the process of reduction, or whether it is to be ascribed to some interaction between the linin and some of the other constituents of the nucleus, it would be unsafe to state definitely at present.

The fifth point lies in the early period at which the longitudinal fission of the linin filament becomes apparent, as compared with the ordinary dividing nuclei of the somatic cells.

The sixth point is the most important of all, namely, that as soon as the number of the developing chromosomes which are about to take part in this mitosis can be counted they are seen to be only one half the number visible at the corresponding stage of the previous nuclear generation, and this number is adhered to in the succeeding nuclear generations until, in the act of fertilisation, it again becomes doubled. Thus, however, we may finally explain it: the reduction in the number of the isolated chromosomes is seen to have been somehow or other brought about during the resting stage of the nucleus, or at any rate in the very early stages of mitosis. And this statement of the matter has been accepted with more or less reservation by most Botanists and Zoologists. Nevertheless we cannot blind ourselves to the fact that certain difficulties do exist in the way of its general application to cover all cases; some of these difficulties are matters of observation, others are questions of theory.

Finally, the seventh point lies in the very remarkable form assumed by the mature chromosome; it often appears as a closed ring which comes to be along the spindle, ultimately splitting across the middle. A careful study of the earlier stages leads however to the conclusion that we are nevertheless really dealing with a true longitudinal fission of the original chromosome rudiment, only the mutual relationship of the parts has been obscured by developmental

<sup>1</sup> E. Sargent, "The Formation of the Sexual Nuclei in *Lilium Martagon*," *Annals of Botany*, vol. x., 1896.

changes. It was owing to the peculiarities of these chromosomes in the Salamander that Flemming gave the name of *heterotype* to this mitosis to distinguish it from the nuclear divisions in the rest of the body. The term Heterotype, or Great Heterotype, has now come into common use to designate the *first* of the two divisions, because although the second *may* resemble the first one, as in Elasmobranch fishes according to Moore,<sup>1</sup> it far more commonly differs widely from it, approximating more or less closely to the form typical for the ordinary somatic nuclear divisions of the organism, as is the case in the Lily divisions. There are, of course, various forms under which the heterotype character of division may appear; but for the most part the net result is clearly a *longitudinal* division of the chromosomes followed by a second longitudinal division in the next mitosis.

I said "for the most part," because there are some apparently well-authenticated exceptions to the general scheme of division which I have just indicated, and they seem to show that in some cases at any rate the process of reduction may be accomplished in a very different way. In certain Crustaceans, Rückert<sup>2</sup> and some other investigators state that in the first of the two divisions with which we are concerned it is true that the number of the chromosomes *appears* to be reduced to one half, and that these undergo longitudinal fission in the usual way; but each of these single chromosomes is really double, and represents two of the original (pre-reduction) chromosomes which have become linked end to end together. The half number then may be said to occur here owing to the incomplete transverse separation of the linin thread, every other transverse separation having been omitted. But as the young (double) chromosome rudiments continue to grow their duplicate nature reasserts itself, and a sort of separa-

<sup>1</sup> Moore, "On the Structural Changes in the Reproductive Cells during the Spermatogenesis of Elasmobranchs," *Quart. Journ. Micr. Sci.*, vol. xxxviii., new ser.

<sup>2</sup> Rückert, "Zur Eireifung bei d. Copepoden," *Anat. Heften, herausgegeben v. Merkel u. Bonnet*, 1894.

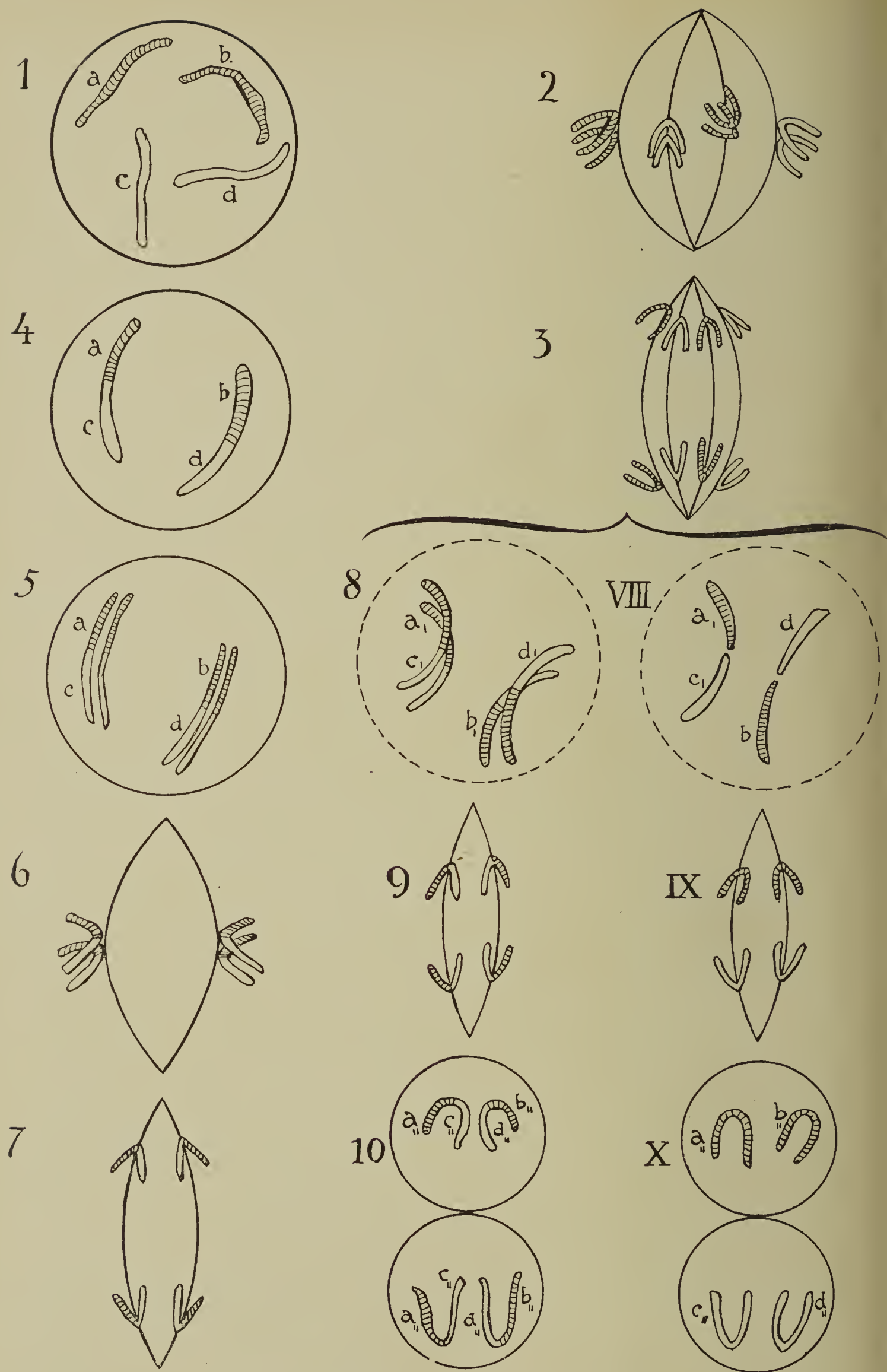


tion eventually takes place. Owing to the previous longitudinal fission and subsequent contraction, the position of each of the duplicate chromosomes is marked by the presence of four spheres. During the first mitosis these are distributed to the daughter nuclei in pairs. During the *second* division the two spheres in each couple separate in like manner, so that after the two divisions each of the four nuclei possess one of the original four spheres. Thus, in this case we are not merely dealing with a distribution of symmetrical quarters of *one* chromosome, but with a distribution of halves of *two entire chromosomes*; that is to say, if we for the moment adopt Weismann's standpoint, the hereditary qualities in this case are *divided* equally between the pair of nuclei which have received halves of *different* chromosomes, whereas if the reduction had been followed by two *longitudinal* divisions of one chromosome, *all* the hereditary qualities would have been distributed to each of the four nuclei.

It is clear that the former method of division, that described by Rückert for Copepods, exactly fulfils the requirements of Weismann's theory by removing one half of the material entities, in which he believes the hereditary qualities to reside, from each of the sexual cells. But it is obvious that, in order to admit the general validity of a reduction division such as seems to be warranted by a study of Crustacea, we ought to find *essentially* the same type of chromosome distribution recurring everywhere. Evidence is not, however, wanting to prove that by no means all organisms do conform to the crustacean type in these important respects, and even the most violent efforts have so far failed to fit them to this Procrustes bed.

In the divisions which result in the formation of the spermatozooids in *Ascaris megalocephala*, Brauer<sup>1</sup> discovered that, whereas in the antecedent mitosis, four chromosomes appeared in the nuclear spindle, in the first of the two divisions we are now considering, only two chromosome rudi-

<sup>1</sup> Brauer, "Die Spermatogenese von *Ascaris megalocephala*," *Arch. f. Mikr. Anat.*, Bd. xlii.



## EXPLANATION OF THE FIGURES.

These figures are intended to illustrate the behaviour of the chromosomes during division. They are all purely diagrammatic.

FIGS. 1-3.—An ordinary vegetative mitosis.

„ 4-7.—The first “reduction” division.

„ 8-10.—The second “reduction” division as it occurs in Plants and in some animals.

„ viii.-x.—The second “reduction” (true) division as it is said to occur in certain animals.

[Figs. 9 and ix. correspond to Figs. 3 and 7, and Figs. 10 and x. illustrate a later stage than is shown in the preceding series.]



ments were present, and that these were split lengthwise into four quarter chromosomes, by two longitudinal planes at right angles to each other. Thus the number of the chromosomes was *already* reduced, but the daughter chromosomes for this and the next division were provided for. According to Boveri, who is supported by other investigators, the same thing probably occurs also in connection with the formation of the ova in the same animal. Again, in the Salamander, as Flemming showed, the first division is a longitudinal one, although owing to the complexity introduced by the formation of closed rings, it at first sight might seem to be a transverse fission. That the second of the two divisions is longitudinal and not transverse is clear, inasmuch as it occurs while the daughter chromosomes of the first divisions are retreating to the poles. In this respect, Salamander offers a fine transitional stage between a normal case in which the splitting takes place at the commencement of the second division, and the instance quoted from Brauer, where the chromosomes undergo a *simultaneous* double fission which is thus effected for the two mitoses at one instead of at two stages. Finally, in the pollen mother cells of such plants as lilies, in which the details of the process have been most carefully worked out by a number of observers, it is clear that the chromosomes which appear in the first division spindle are reduced in number to one half, that these undergo longitudinal fission, and that in the next, and final division which follows rapidly on the first, a second longitudinal division also occurs. These observations have also been repeated on the division of the embryosac, and they have lately been again made the subject of an extremely careful investigation by Miss Sargent,<sup>1</sup> with the result that there is not the slightest evidence in favour of the reduction being in any way brought about by a sorting of the chromosomes as a whole; that is, the reduction as it occurs in these plants does *not* conform to the type as exhibited in the oogenesis and spermatogenesis of Copepods. But if it does not signify whether the chromosomes divide longitudinally or

<sup>1</sup> *Loc. cit.*

transversely, what becomes of the elaborate theories which have been founded upon the assumption of the universality of one or other of these two processes? The believed equivalence secured by a longitudinal fission was supposed to indicate a regular arrangement of the substance of the chromosome of such a nature that, although the composition might vary from one end to the other, the composition of any thin transverse plane could be assumed to be homogeneous. And the alternating discs of strongly and slightly stainable matter described by Balbani<sup>1</sup> in *Chironomus*, and seen by Strasburger in many plants, were thought to be the optical expression of this serial arrangement.

Since Weismann's theory has dominated a great part of cytological investigation, it has been assumed that this structure corresponds to a definite arrangement of the bearers of hereditary qualities. The chromosome is conceived of as a vastly complex structure, made up of small individual units which are grouped in a particular manner. But how does such a theory fit in with those facts concerning reduction which are now before us? It seems that if the chromosomes do really consist of a number of discrete bearers of hereditary qualities, of particles which must themselves be very stable, since the qualities they are assumed to bear are, as a matter of fact, remarkably constant;—it seems that the only way of making room for the fresh qualities introduced at the act of fertilisation is first to get rid of half the number of entire chromosomes from the sexual nuclei. This may be readily imagined in the case of Copepods, but how can we admit it in the other cases I have quoted? But in order to try to reconcile the doctrine of determinants and so forth, with the facts of reduction as exhibited in plants and, at any rate some, animals, it has been suggested that in the resting period before the first division the chromosomes really fuse end to end just as they are said to do in Cyclops, but that they never break asunder again. But this explanation lands us in all sorts of difficulties when we try to work it out. The determinants, biophores and so on, are, *ex hypothesi*, stable

<sup>1</sup> “Sur la structure du noyau des cellules salivaires chez les larves de *Chironomus*,” *Zool. Anz.*, 1882.



bodies in themselves ; consequently, there must be present in each of the reduced chromosomes all the particles which were in the two originals. But it is clear that on this view no real reduction has taken place at all ; the new chromosome cannot be represented as C, but it is still AB and so on through the successive generations—this however is obviously impossible. But if it be urged that in the new chromosome, AB, there is a sort of struggle for existence amongst the hereditary units, half of which become ultimately extinguished, we are carried at once into the realms of pure fancy, and besides, why should not the units have had their fight out before ever the chromosomes were differentiated so that each chromosome in the reduced nucleus merely contains the survivors ? But there is absolutely no evidence that any part of the nucleus does atrophy during these, rather than in other divisions ; indeed, the reproductive nuclei are characterised by their specially large size. Hertwig has tried to get over the difficulty by declining to recognise any such structural arrangement as Weismann and his adherents postulate ; for him the essence of the process lies in the rapid reduction of the nucleus to one fourth of its original bulk, by divisions at right angles to each other. Thus from Hertwig's point of view it does not signify whether these divisions are both longitudinal, or whether one is transverse,—the final result is the same.

And really this seems about to express our present knowledge on the subject. But if we accept such a view, it is difficult to see how we can help giving up a belief in the complicated architectural structure of the chromosome of which each constituent has been supposed to have its special position allotted to it, and its special part to play in the development of the organism. We come very near regarding the chromosome, complicated as it may well be in the structure of its molecules or molecular aggregates, as nevertheless intrinsically symmetrical. Heredity is then the outcome of its constitution *as a whole*, and is not the expression of activities residing in, and apportioned to, respectively discrete parts of it—assuming of course that the chromosomes *are* really the organising directors which

determine the qualities of the animal or plant in which they dwell. But any extended consideration of this topic would open up the question as to the real permanence of the chromosomes throughout the resting nucleus, in which they can no longer be discerned, and would involve an exhaustive discussion of the manner in which they emerge as distinct bodies at each recurring mitosis. And even to touch on the different questions and processes herein concerned would occupy an entire morning. And I think I have already taxed your patience severely enough without putting yet more burdens upon it.

I have tried in the foregoing account to point out how widely opinions differ on the most fundamental questions, the extremes being represented on the other hand by those who see in all organised structures special organs of the cell, which are permanent from generation to generation at least *in posse*, if not *in esse*, and which in some way regulate the changes which recur in cell life; the other side, on the contrary, regards the whole of cell phenomena, including the very "Organs" themselves, as the outcome and expression of forces which have their origin in profound chemical and physical changes as yet beyond our ken. But just as the operation of the forces themselves is transient if periodically recurrent, so also is the existence of some of the so-called organs themselves.

And perhaps in this, as in so many other matters, the middle way is the safest, but I have not sought to follow it because I did not consider it a suitable path for the purposes of a discussion.

"Serpit humi tutus nimium timidusque procellae."

J. BRET LAND FARMER.



## SELECTION IN MAN.

(Continued.)

SINCE the publication of my last article on this subject, Dr. de Cazal has brought out an analysis of the French recruiting returns for seven recent years (1887 to 1893 inclusive).

Examined from the point of view I have been taking, *viz.*, the possibility of natural selection and modification of race-type by way of colour-change, De Cazal's figures do not afford much assistance. It is evident that there is now more laxity in admission, a lower standard of qualification, than was formerly the case; probably, moreover, there has really been an improvement in the physical health of the population generally. Anyhow, the releases on account of infirmities are not half so numerous as they were thirty years ago, while the releases on account of deficient stature have been done away with altogether.

The remissions for France in general averaging 100·4 per thousand, those for the 10 departments with the most blond population were 98·3, those for the 5 most distinctly presenting the combination of blond coloration, long head and tall stature which characterises the North European (Aryan?) type were 97·7, those for the 10 of darkest complexion were 106·8. Here there is no inferiority in the blond type. Let us now see how the exemptions for phthisis and for the euphemisms which often cover it are distributed.

No. of Departments.	Speciality.	Phthisis.	Scrofula.	Faiblesse de Const.	Total.
1 10	Highest stature	1·84	1·75	5·26	8·85
2 10	Lowest „	2·81	3·36	7·06	13·23
3 10 <sup>1</sup>	Blond	1·97	2·28	5·51	9·76
4 10 <sup>1</sup>	Dark	1·59	2·31	6·02	9·92
5 5 <sup>1</sup>	Tall, Blond, Dolich	2·52	1·94	6·64	11·10
6 6	Urban	2·88	2·85	8·50	14·23
7 10	Mountainous	1·83	2·52	6·83	11·18

<sup>1</sup> I have excluded the densely peopled departments of the Nord, Seine Inferieure and Bouches du Rhone.

There is little here to guide us, though the somewhat unfavourable aspect of column 5 is a little suspicious. It may be noted, by the way, that a general high level of stature does not seem to entail a high proportion of phthisical disease, though I have little doubt that in France, as with us, tall young persons suffer more therefrom than short ones in the same community. Knox, who must already have grasped the idea of modification of type by selection, said long ago that the South African Boers were taller than the natives of Holland because among the former the taller youths were not so liable to be cut down by phthisis.

To return—Roberts and Rawson, in their anthropometric report to the British Association, compared the complexional characters of various periods of life, from infancy to extreme old age. The gradual deepening of colour, of hair colour especially, which concurs in most individuals with the advance of years, the earlier age at which greyness is perceptible in the dark haired, and some considerations of minor importance, take away much of the value of Roberts and Rawson's table, carefully digested and widely based though it be. *Primæ facie*, however, it may be claimed as evidence that the changes in colour which do occur are due to development rather than to selection by death.

The possible effect of conjugal selection has been tested by myself, but very insufficiently. My observations tended to show that, among the working classes of Bristol, women with red and women with black hair did not marry in quite so large a proportion as those with hair of other colours. If this were to continue through several generations, we should have a diminution of the two most abundant kinds of hair-pigment (Sorby), and a general prevalence of dull shades of brown. De Lapouge<sup>2</sup> quotes De Candolle to the following effect: 158 brown-eyed men espoused 52 per cent. of women of like colour with themselves, and 48

<sup>1</sup> *Races of Britain*, p. 226.

<sup>2</sup> *Les Selections Sociales*, par G. Vacher de Lapouge, p. 202, Paris, 1889.



per cent. of women with blue or grey eyes. Now there are 44 per cent. of brown eyes among the women of French-Switzerland, so that it seems as though the brown eyes were more attractive. Similarly, 167 men with blue or grey eyes married 59 per cent. of brown-eyed women, which is much above the proportion in the women of the country.

De Candolle<sup>1</sup> found that while 72 couples having both dark eyes gave birth to 3·07 children on an average, 131 couples having both light eyes had only 2·72. He notes that children who were under 10 years of age at the period of observation were not counted; but this fact detracts very little from the value of the observation, which would lead one to expect the rapid diminution of light eyes, and probably also of the blond type. The number of cases, though considerable, is perhaps hardly large enough to support a conclusion of such magnitude. And Mr Galton, on the other hand,<sup>2</sup> dealing with a much larger number of cases, comes to the conclusion that he may "disregard the current popular belief in the existence of a gradual darkening of the British population," and regards eye-colour as "statistically persistent". Mr. Galton's method of working, however, is backwards, from children to parents and grandparents, and therefore takes, I apprehend, no account of the number of barren couples, which, if we could ascertain it, might possibly modify this conclusion. His figures are as follows (summarised):—

	MALES AND FEMALES.			
	Blue.	Grey.	Neutral.	Dark.
First Generation	35·9	27·3	10	26·6
Second    ,,	29·4	31·3	12·1	27
Third     ,,	28·5	32·3	14·7	24
Children	29·6	28	19·4	23·3

Now Mr. Galton, by an examination of the pedigrees of neutral-eyed persons, finds that they may fairly be taken as the offspring, roughly speaking, of parents of whom two-thirds had light and one-third dark eyes. And if we

<sup>1</sup> *Revue d'Anthropologie*, p. 265, 1887.

<sup>2</sup> *Natural Inheritance*, cap. viii., and table xv.

divide the neutrals on this principle, we shall find that we have in the first generation 29·9, and in the last 29·8 of dark hair.

It is often asserted that the milk of brunets is richer in solids than that of blonds ; but I do not think the statement, though not improbable, rests on any sound foundation.

So far our inquiry leads one to suspect a certain degree of physical inferiority in the blond constitution, which may possibly be operating towards the gradual diminution of this type. Let us now try a comparatively uncultivated branch of the subject.

I have examined a large quantity of material derived from the serial volumes of the *Police Gazette*, or *Hue and Cry*. These contain the lists of deserters from the Army, Militia, Marines and Royal Navy, with their names, stature, complexions, occupations and alleged birthplaces. I must allow, *in limine*, that these deserters are themselves the product of successive selections, and are therefore not altogether trustworthy representatives of the general or lower-class population. They are not conscripts, but volunteers ; moreover, these volunteers have been again sifted by the medical rejection of the physically unfit, and these deserters are the product of a third selection implying possibly moral if not physical qualities of a kind differing from those of the soldiers who do not desert. Still, after all this has been said, there is a good deal of internal evidence to lead one to think of them as not a mere heterogeneous collection, but something approaching to a sample of the classes they belong to.

I have taken great pains to eliminate the personal equation of the medical observers, by using the returns for a number of years, scattered over the period from 1845 to 1885, and have rejected any returns which seemed to bear evidence of careless and slovenly observation.

I have also abstracted and analysed the lists of convicted or suspected criminals, of runaway convicts during the period of transportation to Australia and Tasmania, and of men discharged from the Army with disgrace.



My results, if not striking, are curious. Thus, classifying the deserters by their occupations, we have :—

		No.	Index of Nigrescence.	Prop. of Light Eyes.
All Occupations	England	8380	+ 5.57	61.1
	Wales	700	+ 16.85	56.6
	England and Wales	9180	+ 6.37	60.8
	Scotch	1733	+ 8.08	72.2
	Irish	2275	+ 18.85	70.2
	Irish by name, born in Great Britain	733	+ 22.24	69.8
	England (later series)	3500	+ 5.90	61.7
Grooms	English	300	— 5.30	70.3
Butchers		72	— 6.90	66.6
Smiths, Carpenters, etc.	English and Welsh	250	+ 6.6	63.6
Clerks	English	125	+ 2.4	54.4
Do.	{ English, Welsh and Scotch }	400	+ 10.2	59.7
Tailors and Shoe- makers	{ English and Welsh birth and names }	425	+ 13.4	57.8
Country-born Labourers	{ English (pure), largely from S.E. }	1010	+ 1.8	60.1
Country-born Artisans	{ Do. }	340	+ 7	58.4
Town-born Labourers	{ English (pure) }	550	+ 6.3	64.3
Town-born Artisans	{ Do. }	300	+ 10	59.3
Irish-born Labourers	{ Irish }	400	— 3	74.5
Do. of other Occupations	{ Irish }	180	+ 15	70.5
English-born Labourers	{ Irish by name }	60	+ 16.6	75
English-born other Occupations	{ Do. }	65	+ 23.1	75

The index of nigrescence is gotten by subtracting the instances of red and of fair hair from those of dark brown and of black, doubling the black on account of its greater potency. Thus (2 Black + Dark Brown) — (Red + Fair) = Index. The brown are omitted as neutral.

Examination of this table raises a presumption that there is some kind of moral selection or natural bias, which induces a certain number of the dark-complexioned men to betake themselves to sedentary and indoor employments, while

certain blond prefer the outdoor employments connected with the land or with the care of animals. The case of the grooms is pretty distinct and founded on a tolerably broad basis, and both it and that of the butchers agree with my personal observations. The passion for "horse-flesh" and skill in the management of horses does seem to be in some degree hereditary and even racial. The Scandinavians had it, though the natural conformation of their native country was unfavourable to its indulgence; and Australian blacks, who have been but just introduced to the animal, speedily become expert and daring riders.

The apparent difference between the Irish labourers and artisans deserves some comment. The numbers are of course rather small—only sufficient to raise a suspicion that they indicate a fact. The difference assuredly does not represent that of Catholic and Protestant, of exotic and indigenous Irishman. For, as I have shown elsewhere, that difference is of the opposite kind, the exotic, who is often Protestant, being slightly oftener blond than the aborigine, who is almost always Catholic. The men here described as "Irish-born labourers" are largely of the peasant or small-farming class. The "English-born Irish" are probably in race-type *ipsis Hibernis Hiberniores*, for having all true Irish surnames they are of indigenous Irish and not of exotic descent, so far at least as surnames are a guide, which in this particular case they are to a considerable extent.<sup>1</sup>

I have chosen tailors and shoemakers as specimens of the sedentary artisan class, and as being tolerably evenly distributed throughout the country, though the shoemakers of late years, since the partial concentration of the industry in a few large towns, are less so than the tailors. A comparison of tailors from Cornwall with grooms from Yorkshire or Norfolk would be of little avail. It will be observed

<sup>1</sup> It is not simply that a Sullivan or an O'Donnell or a Connellan *must* be Irish by remote paternal descent; that is little; but that as exotic surnames are comparatively few in the western half of Ireland, and as religious differences count for something in matrimony, the maternal is likely to have very largely resembled the paternal ancestry.



that the tailors and shoemakers include a large proportion of dark men. I have tested also to some extent the painters, plumbers, etc., the weavers, the colliers, the smiths and carpenters. The first seem to yield figures resembling those of the tailors; the colliers include many blond men; but they and the weavers are unsatisfactory by reason of their local distribution. The number of the middle and upper class recruits is small; they are included here among the clerks. The higher classes in England and Ireland, so far as my observations go, are rather on the blond side of the general average of the populations, but the present investigation yields nothing in support or explanation of this.

“Legal selection,” says De Lapouge, “ought to operate so as to prevent the criminal from mischief, and to suppress his posterity.” Of course at present we do this very imperfectly; and our failure to do it has and will long have disastrous effects; still our action has probably some force in that direction. That certain physical types tend towards criminality is generally acknowledged, though some criminal anthropologists may be too hasty in defining them. In this country more criminals than honest men are of dark complexion. Thus Roberts and Rawson<sup>1</sup> supply material for the following table, which includes the whole British Isles—

	Index of Nigrescence.	Prop. of Light Eyes.
General population <sup>2</sup>	+ 1·0	66·2
Criminals in prison	+ 8·3	56·4
Lunatics in asylums	+ 5·1	66·9

Here the criminals have about 54 per cent. of dark hair against  $50\frac{1}{2}$ , and 10 per cent. more of them have dark eyes. Red hair appears in smaller proportion than is usual. These characteristics run through the statistics of the four countries without much variation.

The following data are abstracted and summarised from the *Police Gazette* for several years :—

<sup>1</sup> *Final Report of the Anthropometric Committee*, p. 21.

<sup>2</sup> These figures are not strictly comparable with those I have been analysing, the mode of collection having been different.

## CRIMES AGAINST PROPERTY, OR WITHOUT VIOLENCE.

I.	Nationality.	Index.	Light Eyes.	<sup>1</sup> Neutral Eyes.
250 Male Criminals	{ English or Welsh }	+ 28·2	62·8	
500 „ Supervisees <sup>2</sup>	{ birth and name }	+ 21·2	59·4	4·0
100 „ Supervisees	English, pure	+ 14	49	
200 „ „	{ In England, but }	+ 16·5	62·5	
300 „ „	{ of all births }	+ 14·6	58·3	6·3
100 „ „	Irish in England	+ 19	68·2	2
100 Juvenile Males	English	- 1·5	55·3	
100 Adult Females	English	+ 13	49	
200 „ „	All nationalities	+ 16·5	62·5	2·5
100 „ „	Irish in England	+ 25	68	2

The evidence of this table, so far as it goes, runs in the same direction as that of Roberts and Rawson's report. It will be observed that the inclusion of Scotchmen tends to increase the proportion of light eyes, while that of Irishmen generally increases also the index of nigrescence. The figures relating to juvenile criminals are significant, these being often so by hereditary right. The hair index is light, owing to the immaturity of the subjects; but the large proportion of dark eyes is remarkable. Possibly, however, this may be due to their being largely natives of the slums of great cities. I cannot test this suggestion, having no data relating to homologous children not criminal.

The next table has been constructed from records of the colour of the hair and eyes of transported convicts, who had escaped from their allotted place of service during several years previous to and including 1852.

## CRIMINAL FUGITIVES.

		Index.	Light Eyes.	Neutral.	Dark.
200 Males	All Nationalities	+ 27·5	43·5		56·5
500 „	English, Welsh, Scotch	+ 31·2	52·6		47·4
400 „	English	+ 28·3	44·2	14·2	47·6
30 „	(Included above) London	+ 43·3	30		70
50 „	Irish	+ 42	66	8	26
50 Females	All Nationalities	+ 46	36		64
87 „	English, Welsh, Scotch	+ 43·9	58·5		41·5
21 „	Irish	+ 62	66·6		33·3

<sup>1</sup> Most of the observers seem to classify these among the dark eyes.

<sup>2</sup> Persons kept under supervision by the Police after discharge from prison.



These unfortunates, who may be taken to represent generally the quintessence of criminality, show a great tendency to darkness in both eye and hair. This is perhaps least marked in the Irish men, who also average more than an inch in stature beyond the rest. No doubt a larger proportion of them did not belong to the professional or hereditary class.

The subject of convict genealogy is a sore one with our Australian cousins, who certainly did all they could to cut off the current at its source by refusing to receive fresh supplies. The (probably) prevalently blond types of the free immigrants seem to have asserted themselves victoriously. The typical bushman is tall, blond rather than dark, and freckled. Of 35 Australasian deserters the index of nigrescence was  $-8\cdot5$ ; and the proportion of light eyes  $57\cdot1$  per cent.

CRIMES OF VIOLENCE.

		Index.	Light Eyes.	Neutral.	Dark.
88	Males { English and Welsh, a few Scots }	+ 36·3	46·6		53·3
237	" {                 "                 } including the above }	+ 40·1	not stated		
70	"                 Irishmen	+ 42	60	2	37
67	" { Rape, and similar offences, all Nationalities }	+ 37	62		38

In the last category both red and black hair are strongly represented; in the others black, but not red. Nothing like this is observable in any of the lists of criminals against property or without violence ; and I do not think this discrepancy can be accidental. The average stature in the violent criminals seems to be good, but in many cases it is estimated, not measured, and estimates of this kind are more often in excess than otherwise.

Yet another class of evil-doers, not precisely criminal, however, may be found in the men discharged from the army "with ignominy," or "as worthless and incorrigible". A series of these, numbering 200, yielded me an index of nigrescence of 7 per cent., and 63 of them had light eyes. They evidently differ from the ordinary criminal classes:

many of them are blond, and their average stature is fully up to or over the standard of ordinary deserters, and of course very much over that of ordinary criminals. Apparently the men who give the prevailing character to this class are drunkards, unstable, untrustworthy, insubordinate, have in fact the vices of the sanguine temperament, while the typical violent criminal, with his dark complexion, is choleric or melancholic, and the typical perpetrators of sexual offences are choleric or sanguine.

Criminal anthropologists as a rule assign great importance to one or other of two hypotheses, that of atavism and that of degeneration. Lombroso might derive some support from my facts for the former belief. Mr. MacRitchie, who thinks he has proved the historical existence and numerical importance, in earlier days, of whole tribes of outlaws of gipsy type, might deduce some of my criminals from them. Something of the sort may apply to the criminals of violence, to enough of them, that is, to give the apparent colour to the whole mass. But the ordinary criminal, so far as he is not the product of contemporary surroundings, looks more like a product of degeneration. The mean stature is conspicuously low both in my ordinary malefactors, and in the Australian fugitives. As to the cephalic development I have unfortunately no data, and it is probable that in this country at least it is less characteristic than the facial physiognomy, of which Mr. Galton has given us some very striking composite photographs. Meanwhile, we must wait to see what Dr. Garson's investigations may lead to. What is most required, and what most criminal anthropologists have somewhat neglected, is to ascertain the ordinary physical standard of the classes whence criminals arise, and thus to obtain a basis of comparison.

The effect of what De Lapouge styles "legal selection," that is, the temporary or permanent incapacitation of the criminal to propagate his kind, is at present very small. During many years, and indeed many generations, attempts were made to eliminate the criminal type from the British Isles, at the risk of its propagating itself with augmented



rapidity in America or Australia. I have already said that in the latter country the attempt does not seem to have been so perniciously successful as might have been anticipated or feared. And in our own islands social conditions seem to step in where legal ones fail, and the criminal by degeneration is not as a rule highly reproductive. Here we seem to have discovered an agency which may tell a little in favour of the blond, who is menaced with gradual extinction by other processes.

The kephalic index, however, is a much more promising test in matters of selection than the colour of the hair and eyes. In England, indeed, less can be expected from it than in some other countries, owing to the fact that most of *our* race-types are more or less dolichokephalic, and therefore not to be readily distinguished by the simple application of the callipers. But De Lapouge in France, and Ammon in Belgium, have developed and worked this method with ingenuity and success, some of their results being unexpected and indeed wonderful. Of these I hope to give an account in my next communication.

JOHN BEDDOE.

## THE GLOSSOPTERIS FLORA; AN EXTINCT FLORA OF A SOUTHERN HEMISPHERE CONTINENT.

THE last phase of the Carboniferous period in the Northern hemisphere was marked by widespread forests stretching over a considerable tract of country, intersected by shallow lagoons or the remnants of a former sea, on the floor of which were built up thick masses of limestone in the earlier part of the Carboniferous Epoch. A succession of sandstones, shales and coal seams, marks the position of this ancient forest, and from the fossil plants of the Coal Measures we learn that the vegetation was characterised by a general uniformity in the plant types. Gigantic Vascular Cryptogams, such as *Calamites*, *Lepidodendra*, *Sigillarieæ*, numerous ferns, and extinct forms agreeing in the structures of their wood with present-day coniferous and cycadean plants constituted the greater part of this Palæozoic flora. In the succeeding Permian period the vegetation retained in many respects the character of the Coal Period forests; some genera had become extinct, and others became more abundant or appeared for the first time. From Arctic latitudes, through Europe, North America and China the fossil remnants of this Permo-Carboniferous vegetation have been found in abundance, and from the Zambesi district of Africa typical Coal Measure genera are recorded.

Passing further south, we find in South America, Africa, India and Australia, sedimentary deposits which it is believed represent fragments of a Southern hemisphere Continent. In these beds certain forms of plants are met with in considerable abundance, and the botanical evidence distinctly points to the existence of a widely distributed flora differing in its most characteristic types from the contemporaneous vegetation of the North. The Southern plant beds are in part of Permo-Carboniferous and Triassic age.



With one or two exceptions, the Northern Palæozoic forms are not met with in this Southern vegetation. In Australia, more particularly, a few well-known Carboniferous plants have been found, but these belong to a period represented in Europe by rocks anterior to the Coal Measure epoch.

In South America and lately in South Africa one or two Coal Measure genera have been discovered, but, generally speaking, the flora of this Southern Continent is characterised by such genera as *Glossopteris*, *Gangamopteris*, *Næggerathiopsis* and other plants, some of which are absent from the Permo-Carboniferous vegetation in the Northern hemisphere, and others play but a very insignificant part in the composition of the flora. The object of this article is to give a brief summary of this Southern vegetation.

In 1828 the French palæobotanist Brongniart<sup>1</sup> figured and described some tongue-shaped and reticulately veined leaf impressions under the generic name of *Glossopteris*.<sup>2</sup> These fossil leaves are abundant in Australia, and had previously been regarded by travellers as specimens of the well-known *Eucalyptus*. Some of the species included by Brongniart in this genus have since been transferred to other genera, e.g., *Glossopteris Phillipsii* Brong. from the Lower Oolite of the Yorkshire coast is now known as *Sagenopteris Phillipsii* (Brong.). The type species, *G. Browniana* Brong., still remains one of the best-known examples of the genus. The specimens on which this species was founded were from Australia and India, and Brongniart speaks of the leaves from the former country as *G. Browniana* var.  $\alpha$  *Australasica*, and those from the latter as *G. Browniana* var  $\beta$  *Indica*. He describes the Australian forms as smaller in size, subspathulate and obtuse, and the Indian leaves as larger and possessing a lanceolate

<sup>1</sup> Brongniart (1), p. 222, pl. lxii.

<sup>2</sup> He defined the genus as follows: "Folia simplicia, integerrima, sublanceolata, basi sensui angustata, nervo medio valido apice evanescente percursa; nervulis obliquis arcuatis æqualibus, pluries dichotomis vel basi quandoque anastomosantibus et reticulatis".

and acute apex. *Acrostichum*, *Aspidium*, and other recent ferns are compared with the fossil genus, and in one example of *Glossopteris* certain ill-defined spots are spoken of as traces of rounded groups of sori. Since Brongniart's diagnosis was published thousands of *Glossopteris* leaves have been discovered in India, Australia and Africa, but we are still in doubt as to the precise affinities of the genus. Several writers have described markings on leaves which they refer to as sori, but it is extremely doubtful whether these supposed fructifications are of any botanical value. In 1861 Bunbury<sup>1</sup> described some leaves of *Glossopteris Browniana* from India on which were "small round spots very regularly arranged in one or two rows parallel to the margin". The specimens figured by Bunbury are in the Museum of the Geological Society of London; an examination of the fossils shows that the supposed sori have the form of irregularly circular holes in the leaf lamina, bordered by a narrow brown rim, and distributed with but little regularity. The figures 1 and 4 of Bunbury's paper (pl. viii.) convey a very fair idea of the appearance which he describes.<sup>2</sup> It may be that the patches are merely holes in the leaf, and not the impressions of sori, but it is impossible to speak very decidedly as to their real nature. In the absence of any trace of sporangial impressions, we cannot accept the specimen as affording any trustworthy evidence of the nature of the fructification of *Glossopteris*.

In 1872 Carruthers described an Australian form of the same species, in which he noticed "some indications of fruit in the form of linear sori running along the veins and occupying a position somewhat nearer to the margin of the frond than to the midrib".<sup>3</sup> Unfortunately no figure is given of this supposed fertile leaf. Some years later Feistmantel described another type of fructification in which "the secondary veins quite close to the leaf margin seem to pass into an intra-marginal longitudinal vein, leaving thus a very narrow empty space along the margin, which perhaps

<sup>1</sup> Bunbury.      <sup>2</sup> No. 10,356 in the Geological Society's Collection.

<sup>3</sup> Carruthers (2), p. 6.



shows that in fertile fronds the fructification was a marginal one, like the fructification of *Pteris*".<sup>1</sup> On the strength of these discoveries, Feistmantel instituted three groups of *Glossopteris* founded on the nature of the sori. Carruthers' specimen of *G. Browniana* from Australia is the type of Group 1, and is compared with the recent genus *Anthrophyum*; of Group 2, *G. indica* Schimp. is the type, and is compared with *Polypodium*, while Group 3 is represented by Feistmantel's examples of *G. augustifolia* with the *Pteris*-like fructification. It has recently been pointed out<sup>2</sup> that this classification of Indian and Australian forms has been further complicated by the discovery of the Indian type of sori in Australian leaves.<sup>3</sup> The fragment responsible for this supposed complication is imperfectly preserved and shows on its surface three "sub-oval convex impressions," which cannot be accepted as genuine traces of sporangia. In referring to this discovery, Etheridge remarks that the supposed sporangial groups do not convey to him the idea of sori, but adds: "We must however bow to the evidence, such as it is, and it would thus appear that we have in Australia *Glossopteris*-like leaves possessing two out of three forms of fructification".<sup>4</sup> If evidence is unsatisfactory it is hardly a matter of duty to accept it, or to deduce from it far-reaching conclusions! On the whole, it would seem the safer course to admit that as yet no trustworthy example of a fertile *Glossopteris* frond has been recorded from either India or Australia, and we have certainly no data on which any classification can be legitimately founded.

Until we possess leaves showing distinct sori and sporangia it is of little use to institute a comparison of the sterile fronds with those of recent ferns. The leaves of species of the polypodiaceous genus *Anthrophyum* agree very closely in form and venation with *Glossopteris*; in some species from Fiji there is little or no midrib; in others from South America the midrib may extend to the leaf tip. In the fertile fronds the sporangia occur in continuous lines,

<sup>1</sup> Feistmantel (2), p. 97.

<sup>2</sup> Etheridge (4).

<sup>3</sup> Mitchell.

<sup>4</sup> Etheridge (3), p. 237.

following the course of the veins on the under surface of the lamina, such a frond imperfectly preserved as an impression would probably convey the idea of fairly broad veins rather than of rows of sporangia. The genera *Acrostichum*, *Hemionitis* and others afford close parallels with *Glossopteris* as regards shape and venation.

Another well-known fossil often associated with *Glossopteris* is the genus *Vertebraria*, founded by Royle in 1829.<sup>1</sup> He proposed this name for some Indian fossils which are figured in his work on the *Natural History of the Himalayas*, and described the specimens under two specific names, *V. indica* and *V. radiata*. No real specific difference can be detected in the examples figured. Bunbury, Feistmantel and other writers have given more complete descriptions of this genus; a typical specimen usually presents the appearance of a long cylindrical structure varying in breadth from a quarter of an inch to an inch, occasionally branched, and the axis marked by a median line from which offshoots pass off at intervals to the margin of the fossil.

Bunbury was the first to suggest that the *Vertebrariae* might be the roots of some large plant.<sup>2</sup> The specimen on which Bunbury's opinion was based is in the Museum of the Geological Society; it shows the numerous roots remarkably well and the figure hardly does justice to this unusually interesting example of the genus.<sup>3</sup> Until quite recently we have been absolutely in the dark as to the nature and relationship of this fossil. Zeiller<sup>4</sup> has now brought forward good evidence that *Vertebraria* is the rhizome of *Glossopteris*. From an examination of specimens recently found in the Beaufort beds of South Africa he has been able to trace a connection between *Glossopteris* and *Vertebraria*; he finds that the median veins of the former are continued as transverse grooves in the axis of the latter. The median line occupying the axis of a *Vertebraria* would thus be the central stele and the lateral offshoots leaf-

<sup>1</sup> Royle, p. xxix.\*, pl. ii.

<sup>2</sup> Bunbury. The specimen figured by Bunbury (pl. xi., fig. 3), now in the Geological Society's Museum, shows the roots remarkably well.

<sup>3</sup> Bunbury, pl. xi., fig. 3.

<sup>4</sup> Zeiller (5).



trace bundles. There are also reasons for believing that the stem of *Glossopteris* bore two kinds of leaves, the ordinary tongue-shaped fronds and much smaller scale leaves. Zeiller compares *Struthiopteris Germanica* and *Oleandra* with *Glossopteris*, both as regards the arrangement of leaves on the stem and the distribution of vascular strands in the rhizome.

In spite of the fact that in some districts beds of rock extending over a wide area are literally made up of *Glossopteris* leaves, these are almost without exception detached fronds and not attached to any stem structure. In Africa beds of shale are frequently found to be almost entirely made up of *Glossopteris* fronds, and in Australia<sup>1</sup> beds of clay have been described as owing their foliation to the close packing of the leaves of this fern. In 1849 Dana<sup>2</sup> figured an example in which several fronds appeared to be given off from a stem fragment, and another specimen has now been figured by Etheridge<sup>3</sup> from New South Wales. In the latter case several lanceolate fronds, which agree in outline with *Glossopteris linearis* McCoy, and *G. Clarkei* Feist., are attached to the apex of a comparatively broad stem. The surface of the stem is covered with crowded leaf-scars, and an internal cast shows numerous narrow protuberances which probably represent the leaf-trace bundles. The general appearance of the stem does not agree at all closely with that of *Vertebraria*, which Zeiller has shown to be the rhizome of some forms of *Glossopteris*. It is probable, therefore, that there was more than one form of rhizome bearing true *Glossopteris* leaves.

The wide distribution and extended geological range of *Glossopteris* in the Southern hemisphere is a fact well known to geologists, and of considerable interest from the point of view of the distribution of fossil plants, and the development of ancient floras. The term *Glossopteris* flora originally proposed by Neumayr, has come to be employed for an assemblage of plants ranging from the Upper Palæozoic to Lower Mesozoic strata, and char-

<sup>1</sup> Dana, p. 716.

<sup>2</sup> Dana, pl. xii., fig. 13 C.

<sup>3</sup> Etheridge (3).

acteristic of the Southern hemisphere. Feistmantel<sup>1</sup> has objected to the use of the term *Glossopteris* flora on the ground that the genus *Glossopteris* extends to the Rhætic and Jurassic beds, and is not confined to the Permo-Carboniferous rocks which are usually the strata to which Neumayr's term is applied. With the exception of a species of *Glossopteris*, *G. Browniana*, var. *Australasica*, described by Zeiller from the Rhætic beds of Tongking,<sup>2</sup> no typical example of the genus appears to have been recorded from any locality north of Northern India. A very imperfectly preserved impression figured by Trautschold from Russian Lower Cretaceous beds under the name of *Glossopteris solitaria*<sup>3</sup> affords no proof whatever of the occurrence of that genus. The Tertiary plant referred to this genus by Visiani and Massalongo in 1858<sup>4</sup> cannot be accepted as an undoubted example of this Southern hemisphere fern.

Having given some account of the typical member of the *Glossopteris* flora, we may pass on to describe very briefly the most important districts in which this assemblage of plants occurs.

INDIA.—Occupying a vast area in Bengal and Central India, there is a series of beds of fluviatile origin, containing few animal remains, but fossil plants in abundance. This enormous mass of river sediments constitutes what Medlicott has termed the Gondwana series, the name being chosen from the occurrence of the rocks in a district south of the Narbadá Valley, which it is supposed was formerly inhabited by the aboriginal Gond tribes.<sup>5</sup> In speaking of this series in his presidential address at the Montreal meeting of the British Association, Blanford<sup>6</sup> draws attention to the unusual interest of the Gondwana beds “on account of the extraordinary conflict of palæontological evidence” afforded by the fossil plants and animals. The Gondwana beds are divided into two groups, the Lower and Upper, distinguished from one another by well-marked

<sup>1</sup> Feistmantel (5), p. 13.    <sup>2</sup> Zeiller (1).    <sup>3</sup> Trautschold, pl. xix., fig. 1.

<sup>4</sup> Visiani and Massalongo, p. 206, pl. i., fig. 1.

<sup>5</sup> Oldham.

<sup>6</sup> Blanford (1), p. 696.



stratigraphical and palæontological breaks. It is with the lower divisions that we are at present concerned; this includes three series, at the base the Talchir and Karharbári beds, followed by the Damuda and Panchet series.

LOWER GONDWANA.	{	Panchet.	{	Ranigunj and Kámthi.	
		Damuda.		Barákár.	
		{		{	
				Karharbári.	
				Talchir.	

The Talchir and Karharbári beds consist of shales, sandstones, conglomerates and coal seams. Towards the base of the series boulder beds occur over a wide area, made up of fine silt full of rounded and subangular striated rocks, varying in size from  $\frac{1}{4}$  inch to 15 feet in diameter. In some places the boulder beds rest on a platform of older rocks exhibiting the polished and striated appearance of an iceworn surface.

The following species of plants may be mentioned from this horizon :—<sup>1</sup>

<i>Schizoneura cf. Meriani</i> , Schimp.	<i>Glossozamites Stoliczkanus</i> , Feist.
<i>Vertebraria indica</i> , Royle.	<i>Næggerathiopsis Hislopi</i> (Bunb.).
<i>Gangamopteris cyclopteroides</i> , Feist.,	<i>Euryphyllum Whittianum</i> , Feist.
and other species of the genus.	<i>Voltzia heterophylla</i> , Brong.
<i>Glossopteris Communis</i> , Feist.	
<i>G. indica</i> , Schimp., and other	
species.	

*Damuda series*.—This important group of rocks consists of sandstones, shales and seams of coal, from which a fairly rich flora has been obtained. The following may be given as characteristic species :—<sup>2</sup>

<i>Schizoneura gondwanensis</i> , Feist.	<i>G. Browniana</i> , Brong., and other
<i>Phyllothea indica</i> , Bunb.	species.
<i>Trizygia (Sphenophyllum) speciosa</i> ,	<i>Gangamopteris cyclopteroides</i> , Feist.,
Royle.	and other species.
<i>Vertebraria indica</i> , Royle.	<i>Belemnopteris Woodmasoni</i> , Feist.
<i>Sphenopteris polymorpha</i> , Feist.	<i>Sagenopteris polyphylla</i> , Feist.
<i>Alethopteris Whitbyensis</i> , Göpp.	<i>Pterophyllum burdwanense</i> , McCl.
<i>Macrotaeniopteris danæoides</i> , Royle.	<i>Næggerathiopsis Hislopi</i> (Bunb.).
<i>Glossopteris communis</i> , Feist.	<i>Voltzia heterophylla</i> , Brong. Etc.,
	etc.

<sup>1</sup> For figures of these plants see Oldham and Feistmantel (1).

<sup>2</sup> See Feistmantel (2).

Of the above fossils, *Glossopteris* and *Vertebraria* are the most abundant, Cycads and Conifers being exceedingly rare.

From the overlying *Panchet* group, several fossil animals, but few plants, have been recorded :—

*Schizoneura gondwanensis*, Feist.

*Glossopteris communis*, Feist.

*Vertebraria indica*, Royle.

*G. indica* and other species.

In the extra-peninsular area boulder deposits and fossiliferous marine strata occur in the Salt Range, N.W. Afghanistan and other districts homotaxial with the Lower Gondwana Rocks of the Indian Peninsula. The Salt Range beds<sup>1</sup> are of special interest as having afforded trustworthy evidence as to the geological age of the Lower Gondwana strata; from the marine beds typical Carboniferous fossil shells have been discovered of the same species as Australian and European forms. Of these, *Conularia lævigata*, *Conularia tenuistriata*, *Plemeotomaria nuda*, *Cone-tes cracowensis* and other species occur in the Salt Range and in marine strata of New South Wales. The question of the geological age of the Salt Range beds has given rise to considerable controversy, but now it is generally admitted that the boulder beds of this area and those of the Talchir series are homotaxial, and of Permo-Carboniferous age.<sup>2</sup>

AUSTRALIA.<sup>3</sup>—In New South Wales, Victoria, Queensland, Tasmania and other districts the *Glossopteris* flora is abundantly represented, and, as in India, glacial beds are associated with the lowest strata containing members of this flora. Confining our attention to rocks below the Mesozoic System, the beds have been classified as follows in New South Wales :—

Wianamatta Shales.

Hawkesbury Sandstones.

Newcastle beds, or Upper Coal Measures.

Upper Marine beds with Carboniferous fauna

Stony Creek beds, or Lower Coal Measures

Lower Marine beds with Carboniferous fauna

} Muree beds.

<sup>1</sup> Oldham, p. 121. See also Waagen, Blanford (2) and (3), Seward, etc.

<sup>2</sup> *Phyllothea* and *Vertebraria* are recorded from the Sarawak Coal in BORNEO. (Posewitz, *Borneo*, p. 290. Translated by F. H. Hatch, London, 1892.)

<sup>3</sup> See Oldham, David, Blanford, Feistmantel (3) and (6), Morris, etc.



*Muree beds*.—The marine strata containing typical Carboniferous fossil shells are of particular importance from the point of view of the correlation of Indian and Australian boulder deposits. The boulder beds of Bacchus Marsh in Victoria are also of the same geological age; they contain few plant remains, but a species of *Gangamopteris* has been recorded identical with one from the Talchir-Karharbári beds. From the Lower Coal Measures of New South Wales, that is the strata intercalated between the marine beds containing typical Carboniferous fossil shells, the following plants are known :—

<i>Phyllothea australis</i> , McCoy.	<i>Glossopteris Browniana</i> , Brong., and
<i>Annularia australis</i> , Feist.	three other species.
	<i>Næggerathiopsis prisca</i> , Feist.

In the Newcastle beds, which agree in age with the Damuda series of India, several species of plants have been found, *e.g.*:—

<i>Phyllothea australis</i> , McCoy.	<i>Glossopteris Browniana</i> , Brong., and
<i>Vertebraria australis</i> , McCoy.	other species.
<i>Sphenopteris alata</i> , Brong., and	<i>Gangamopteris augusti folia</i> , McCoy.
other species.	Etc.

The Hawkesbury and Wianamatta beds need not be dealt with as they are referred to a higher horizon than that which more especially concerns us at present. The occurrence of rocks older than the Muree series is referred to later. In Queensland a series of strata occurs resting unconformably on Devonian Rocks; they have been classified as follows and referred to a Permo-Carboniferous age :—

Upper Bowen.  
Middle Bowen.  
Lower Bowen.  
Star Series.  
Gympie Series.

The flora of the two lowest series is “in no way allied to that which is found in the three succeeding divisions, but possesses a decidedly Carboniferous facies, the distinguishing plant being *Lepidodendron*”.<sup>1</sup> From the Bowen River

<sup>1</sup> Jack and Etheridge, p. 70.

formations the *Glossopteris* flora has been recorded, including the following species :—

*Phyllothea australis*, Brong.      *Glossopteris Browniana*, Brong.  
*Sphenopteris lobi folia*, Morris,    *G. linearis*, McCoy. Etc.  
 and other species.

In Victoria a group of strata known as the Bacchus Marsh Sandstones rests on rocks containing Devonian and Lower Carboniferous plants, and includes extensive boulder beds of undoubted glacial origin. Among the plants recorded are :—

*Gangamopteris obliqua*, McCoy.    *G. Spatulala*, McCoy. Etc.

In TASMANIA<sup>1</sup> plant-bearing beds occur in the Mersey coalfield and in the neighbourhood of Hobart which are correlated with the Permo-Carboniferous beds of India and other regions. *Glossopteris*, *Gangamopteris*, *Phyllothea* and other characteristic genera of the *Glossopteris* flora have been found in these strata.

A valuable addition has recently been made to our knowledge of Australian glacial deposits and rocks of Permo-Carboniferous age by Professor Edgeworth David.<sup>2</sup> He gives an able account of the stratigraphy of Australian districts and throws fresh light on the conditions which obtained during Permo-Carboniferous times.

AFRICA.<sup>3</sup>—Our knowledge of the South African beds is on the whole less satisfactory and more imperfect than in the case of India and Australia. An extensive area of the Cape is covered by a series of sandstones and shales with interbedded coal seams, known as the Karoo series. These rocks “occupy the largest portion of South Africa, as they compose the whole of the interior, forming the high elevated plains of the Kalahari, the Free States of the Transvaal, as well as the countries to the north as far up as the Limpopo; they are also to be met with at the Zambezi”.<sup>4</sup> The Karoo formation has been subdivided as follows :—

<sup>1</sup> Johnston and Feistmantel (3), etc.

<sup>2</sup> David.

<sup>3</sup> Oldham, Green, Mouille (good sections given in this paper), Waagen (1), Jones, Feistmantel (5), Schenck (a good geological Map of South Africa is given by Schenck), De Launay.

<sup>4</sup> Griesbach, p. 57.



Upper or Stormberg bed.

Middle or Beaufort beds.

Lower or Eccca and Koonap beds.

In the Eccca beds boulder deposits occur precisely similar to, and homotaxial with, those of India and Australia. The underlying Table Mountain Sandstones are often marked with deep grooves and exhibit other characteristics of ice-worn rocks. The following plants, among others, are recorded from this horizon :—

*Glossopteris Browniana*, Brong.      *Næggerathiopsis Hislopi*, Bunb.

*Gangamopteris Cyclopteroides*, Feist.      Etc., etc.

From the overlying Beaufort beds we have a flora similar to that of the Indian Damudas and Australian Newcastle Strata.

In a collection of plants recently forwarded by Mr. Draper from a locality not far from Johannesburg, there are numerous *Glossopteris* leaves associated with casts of fairly well-preserved Lepidodendroid or Sigillarian stems. The association of these forms is of special interest, and a more complete examination of the specimens may throw fresh light on some points connected with the distribution of the *Glossopteris* flora. Professor Zeiller<sup>1</sup> has lately described several species, including *Glossopteris*, *Næggerathiopsis*, and others from the neighbourhood of Johannesburg. It is impossible, however, in this summary to do more than mention the facts, but it is hoped to discuss elsewhere the nature of the South African plants in a more complete manner.

SOUTH AMERICA.—In 1889 Mr. Derby<sup>2</sup> recorded the occurrence in the Province of Parana of wide-spread boulder beds similar to those of India and elsewhere. His observations, however, were of a superficial character, and in themselves of little value for purposes of exact correlation. Recently some very important and interesting additions have been made to our knowledge of the geology of this country.<sup>3</sup> In 1869 Carruthers<sup>4</sup> described a number of plants

<sup>1</sup> Zeiller (6).

<sup>2</sup> Waagen (2), letter from Derby.

<sup>3</sup> Blanford (4), Kurtz and Zeiller (4), De Lapparent and Steinmann.

<sup>4</sup> Carruthers (1).

brought by Mr. Plant from the Province of Rio Grande do Sol; Zeiller has now added to this list, and furnished additional facts of special value as regards the geographical distribution of Permo-Carboniferous plants. These Brazilian beds have now furnished the following species of plants :—

<i>Psaronius brasiliensis</i> , Brong. <sup>1</sup>	<i>Lepidophloios laricinus</i> , Sternb.
<i>Lepidodendron Pedroanus</i> , Carr.	<i>Cordaites</i> .
<i>Næggerathia obovata</i> , Carr.	<i>Gangamopteris cyclopteroides</i> ,
<i>Dadoxylon Pedroi</i> , Zeill.	Feist. Etc.
<i>Odontopteris Plantiana</i> , Carr.	

In this flora we have, therefore, plants of the same type as those characteristic of Northern Hemisphere Palæozoic rocks, associated with such a typical member of the *Glossopteris* flora as *Gangamopteris*. From plant-bearing beds in the Argentine Republic, Kurtz has recently recorded the following species :—

<i>Neuropteridium validum</i> , Feist.	<i>Gangamopteris cyclopteroides</i> , Feist.
<i>Equisetites morenianus</i> , Kurtz.	<i>Sphenozamites multinervis</i> , Kurtz.
<i>Næggerathiopsis Hislopi</i> , Bunb.	

Zeiller<sup>2</sup> correctly points out that Kurtz's *Sphenozamites* is probably a form of *Næggerathiopsis*. He considers these Argentine plant beds are of the same age as those of Rio Grande do Sol, and places both on the same horizon as the Karharbári beds of India, the Eccá beds of Africa, and the Bacchus Marsh and Newcastle beds of Australia. Kurtz's paper has been translated and printed in the *Records of the India Geological Survey*,<sup>3</sup> and Blanford<sup>4</sup> gave an account of the recently discovered *Glossopteris* flora in Argentina in a short article printed in *Nature* in 1895.

The fossil plants described by Geinitz<sup>5</sup> and Szajnocha<sup>6</sup> from Argentina are from younger and older rocks, Rhætic and Culm, than those containing representatives of the *Glossopteris* flora.

In South Africa, India and Australia, undoubted glacial deposits occur in close association with strata containing

<sup>1</sup> Brongniart (2).

<sup>2</sup> Zeiller (4).

<sup>3</sup> Kurtz.

<sup>4</sup> Blanford (4).

<sup>5</sup> Geinitz.

<sup>6</sup> Szajnocha (1) and (2).



members of the *Glossopteris* flora. These beds are now referred on good evidence to a Permo-Carboniferous age. In South America similar boulder beds apparently occur, but as to these we possess but little accurate knowledge.<sup>1</sup> In describing the glacial beds of Australia, Edgeworth David writes : "In the case of Australia, Southern Africa and India, the general direction in which the ice moved appears to have been from South to North. In Australia the thickness of the glacial beds (unparalleled, so far as the author is aware, in any other part of the world, being about 2000 feet, if the intercalated beds of sandstone and conglomerate are included in the estimate) implies that the Permo-Carboniferous glacial epoch in the Southern Hemisphere was of prolonged duration."<sup>2</sup> From Bajo de Velis in the Argentine Republic typical species of the *Glossopteris* flora are recorded from beds which are in all probability homotaxial with those of Africa, Australia and India, and of Permo-Carboniferous age. From Brazil we have a flora of a rather different character ; it consists in fact of such genera as *Lepidodendron* and others characteristic of European Carboniferous and Permian rocks, and unrepresented in the typical *Glossopteris* flora. Associated with these Northern Coal Measure genera *Gangamopteris* has been found, and this supplies a connecting link with the *Glossopteris* flora of Argentina and other districts. From New Zealand it would appear that no well-authenticated example of the genus *Glossopteris* has so far been recorded. In China, although Permo-Carboniferous rocks occupy a very considerable stretch of country, and have furnished abundant materials for a detailed monograph on fossil plants by Professor Schenk in Richthofen's *China*,<sup>3</sup> the *Glossopteris* flora has not been recognised in Palæozoic strata. The Palæozoic plants from the coalfields of China agree in the main with the typical Coal Measure forms of the Northern Hemi-

<sup>1</sup> Boulder beds have been described by Derby (*Records Ind. Geo. Surv.*, vol. xxii., pt. ii., p. 69, 1889) in Southern Brazil, and Blanford [Blanford (5)] considers that they are probably of the same age as the plant-bearing beds of Rio Grande do Sol.

<sup>2</sup> David, p. 300.

<sup>3</sup> Schenk.

sphere. It is of interest to note that Zeiller has recognised eleven species characteristic of the European Upper Coal Measures from Carboniferous beds in the coal basin of Tété in the Zambesi region.<sup>1</sup> We see, therefore, that European Coal Measure species are met with in a region far south of the typical Northern areas. From Tongking<sup>2</sup> *Glossopteris* and other genera of plants have been recorded, but the flora is probably of Rhætic age.

From the above lists of fossils and brief descriptions, it must be clear to any one who is but superficially acquainted with the typical Permo-Carboniferous plants of Europe and other parts of the Northern Hemisphere, that there is a striking contrast between the floras of this Geological Epoch in Northern and Southern latitudes. In the former we have *Lepidodendra*, *Sigillariæ*, *Calamites*, *Sphenophyllum*, *Pecopteris*, *Neuropteris*, *Sphenopteris*, and other well-known genera; in the latter these forms are for the most part absent, and in their place the *Glossopteris* flora is met with. On the other hand we have abundant evidence that several European genera of plants were in existence in Southern latitudes prior to the appearance of the Permo-Carboniferous *Glossopteris* flora. In an important memoir by Feistmantel<sup>3</sup> on Australian fossil plants, there are numerous figures of European forms from Lower Carboniferous and Devonian Rocks. From the Mount Wyatt beds of Queensland, or the Goonoo Goonoo beds of New South Wales and the Iguana Creek beds of Victoria, plants have been obtained indicative of an Upper Devonian or transitional horizon. In New South Wales<sup>4</sup> and Queensland plants occur which are referred to Lower Carboniferous European species. The following may serve as examples illustrating the occurrence in Australia of typical Carboniferous-Devonian species:—

<i>Lepidodendron australe</i> , McCoy. <sup>5</sup>	<i>Cordaite australis</i> , McCoy.
<i>L. nothum</i> , Ung.	<i>Archæopteris Howitti</i> , McCoy.
<i>L. Veltheimianum</i> , Sternb.	<i>Rhacopteris intermedia</i> , Feist.
<i>Bothrodendron</i> ( <i>Cyclostigma</i> ) <i>australe</i> , Feist.	<i>R. Septemtrionalis</i> , Feist.
	Etc.

<sup>1</sup> Zeiller (2).    <sup>2</sup> Zeiller (1).    <sup>3</sup> Feistmantel (4).    See also Etheridge (1).

<sup>4</sup> Ross, etc.

<sup>5</sup> McCoy and Etheridge (3).



Several writers record species of *Lepidodendra*, *Stigmara* and other familiar genera from strata underlying the Karoo Series of South Africa. Although many references to Lower Carboniferous plants occur in papers dealing with the Geology of the Cape, our exact knowledge of such plants is extremely small; the specimens are often spoken of as unsatisfactory, and no good figures have so far been published to enable us to form definite opinions as to the nature of the fossils.<sup>1</sup> In the British Museum and in the Museum of the Geological Society there are a few specimens of plants from South Africa which have been referred to different Coal Measure genera, but the material is extremely poor. Some of the supposed Carboniferous forms recorded from South Africa, for example those mentioned by Gray, are most probably specimens from the Coal Measures of Europe.<sup>2</sup> From Culm beds in Argentina Szajnocha<sup>3</sup> describes *Lepidodendra Pedroanum*, Carr., *L. cf. nothum*, Ung., *Rhacopteris cf. Machaneki*, Stur., *Cordaites cf. borassifolius*, Brong., and other forms. Zeiller considers that the plant referred to *Lepidodendron Pedroanum* is identical with the Culm species, *Lepidodendron Volkomannianum*, Sternb. In considering those Southern Hemisphere plants which agree with Culm and Upper Devonian species from Europe, it is important to bear in mind the fact that the *Lepidodendron* examples are in nearly every case partially decorticated stem casts, and cannot therefore be relied on with much confidence in the comparison of specific types. This danger has been pointed out by more than one writer, and Nathorst<sup>4</sup> has recently emphasised the need of caution in his valuable memoir on the Arctic Palæozoic flora. The plants from Bear Island, Spitzbergen, the Kiltorkan grits of Ireland, the Culm of Moravia and Silesia and other districts, afford instances of the striking similarity or even identity between the oldest known plants of Africa, South America and Australia and those from high northern latitudes. In India no plant-bearing beds are known older than the Lower Gondwanas.

<sup>1</sup> See Feistmantel (5), Gray, Green, Rubidge, Bain, etc.

<sup>2</sup> Feistmantel (4), p. 7.

<sup>3</sup> Szajnocha (2).

<sup>4</sup> Nathorst.

Summing up the facts in a few words, there are a few plant genera in Australia, South Africa and South America which agree closely with European Culm and Upper Devonian forms. Above this horizon in India, Australia and Africa the typical European plants are practically unrepresented, and in their place a new flora suddenly makes its appearance, characterised by *Glossopteris* and other genera of ferns and equisetaceous plants. In South America, and probably in South Africa, the European facies seems to have held its ground to a somewhat later period, *Lepidophloios* and other northern genera being found in association with representatives of the *Glossopteris* flora. It is a fact of considerable interest that many of the plants characteristic of the Permo-Carboniferous *Glossopteris* flora not only persist to a later epoch in the Southern Hemisphere, but also extend northwards and occur as fairly common species in European Jurassic beds. To mention a few examples, there is a close agreement between *Næggerathiopsis Hislopi*, Bunb., and a leaf figured by Schorlhausen<sup>1</sup> from Russia as *Rhoptozamites*; the *Glossozamites* pinnæ figured by Feistmantel<sup>2</sup> from India fairly closely resemble similar leaves described by Kurr,<sup>3</sup> Schenk and others from European Jurassic and Wealden strata; the genus *Phyllothea* is a well-known member of the Jurassic flora of Siberia, Italy, England and other countries; also another South Hemisphere equisetaceous plant, *Schizoneura*, occurs in the European Trias.

From some cause, then, it would appear that the Palæozoic vegetation, which in Lower Carboniferous times had a more or less world-wide distribution, was replaced in the South by a new set of plants, while in the Northern Hemisphere the older forms continued to flourish until the close of the Permian epoch, and were then superseded by a flora of a newer facies. The widespread glacial deposits of Australia, Africa, India and South America, point to conditions favourable to the existence of ice and a lowering of

<sup>1</sup> Schorlhausen, pl. xv., figs. 1-11.

<sup>2</sup> Feistmantel (1), pl. xx., figs. 4 and 5.

<sup>3</sup> Kurr, pl. i., fig. 5.



temperature. There is, moreover, good evidence for the existence in Permo-Carboniferous times of a large continental mass of land stretching across from Southern Africa to India, and occupying part of what is now the Indian Ocean. In all probability South America also formed part of this Southern Continent, for which the name of Gondwana Land<sup>1</sup> has been proposed. Over this continent, which formed a land connection between Australia on the one side, and South America on the other, glacial conditions obtained of sufficient extent to give rise to the thick mass of boulder beds already alluded to. It is natural to suppose that there must have been a close connection between the lowering of temperature in Gondwana Land and the occurrence of the *Glossopteris* flora. We may, perhaps, assume that the Palæozoic plant types were unable to exist under the colder conditions, which on the other hand favoured the extension of a flora of a different facies, which may possibly have been derived from an antarctic continent. In speaking of the *Glossopteris* flora and the existence of Gondwana Land, Blanford remarks that perhaps the difference between the Upper Carboniferous flora of the Northern Hemisphere and the contemporary flora of the Southern Hemisphere, may be due to both isolation and climate. He goes on to say, "there is, moreover, some evidence in favour of the view that the transfer of the southern plants to the Northern Hemisphere was caused by a period of low temperature that drove a southern temperate flora northward to the equator".<sup>2</sup> "It is highly probable," he adds, "that many other forms of terrestrial life besides the Mesozoic flora originated in the Southern Hemisphere; and unless a very considerable area of what is now deep ocean was occupied by land in Mesozoic and Palæozoic times, a change in favour of which there appears but slight evidence, it is far from improbable that the antarctic continent was the original area of development." In a later paper the same

<sup>1</sup> Suess, vol. ii., p. 318, see also Blanford (5).

<sup>2</sup> Blanford (3), p. 105, see also Neumayr, vol. ii., p. 191.

author<sup>1</sup> writes: "The discovery in several different parts of South America of *Gangamopteris* and *Neuropteridium*, associated in the same beds with *Lepidodendron*, may perhaps imply that a land connection existed in newer Palæozoic times in the American area between the continent of the Northern Hemisphere and Gondwana Land". A consideration of the full significance of the recent discovery in South Africa of a lepidodendroid plant in association with *Glossopteris* is deferred until the material has been more fully investigated.

In dealing with an assemblage of extinct plants, it is extremely difficult, not to say impossible, to arrive at any definite conclusion as to the climatic conditions under which the different genera and species existed. We cannot adduce any trustworthy evidence from the plants themselves to warrant the assumption that the *Glossopteris* flora was well fitted to withstand a cold climate; but external evidence favours the conclusions as to climatic changes having been in a great measure responsible for the existence of two distinct botanical provinces during the Permo-Carboniferous era. Unfortunately we possess but little exact or complete botanical knowledge of the Southern Hemisphere plants; the work of Feistmantel and others has made us familiar with the various leaf forms characterised in many instances by their large size and anastomosing veins, but we are still without information as to internal structure and reproductive organs of the typical genera of the *Glossopteris* flora.

A more detailed and extended study of the Upper Palæozoic plants of the Southern Hemisphere, and a careful comparison of the homotaxial floras north and south of the equator, should lead to important generalisations interesting alike from the point of view of geographical botany, and the distribution of land and water at the close of the Palæozoic era.

<sup>1</sup> Blanford (5), p. 59.



	AUSTRALIA.			TASMANIA.	SOUTH AFRICA.	SOUTH AMERICA.		INDIA.
	VICTORIA.	NEW SOUTH WALES.	QUEENSLAND.			ARGENTINA.	BRAZIL.	
Permo-Carboniferous.	Bacchus Marsh. Sandstones. <i>Glacial beds.</i>	Muree beds. <i>Glacial beds.</i>	Bowen River Coalfield. <i>Glacial beds.</i>	Mersey Coalfield. <i>Glacial beds.</i>	Kimberley—Ecca beds. <i>Glacial beds.</i>	Bajo de Velis Series.	Rio Grande do Sol. <i>Glacial beds.</i>	Karharbári. Talchiro <i>Glacial beds.</i>
Lower Carboniferous or Devonian.	Avon River. Sandstones. Iguana Creek beds.	Smith's Creek. <i>Lepidodendron</i> beds. Goonoo Goonoo Series.	Drummond Range, Mount Wyatt beds, etc.	Fingal Soft Shales. (No plants.)	Lower Carboniferous ( <i>Lepidodendron</i> ) beds and Zuurbergen—Zwartebergen and Wittebergen beds in Cape Colony. Devonian.	Retamito Series.		No plant-bearing beds.

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[The above list is very far from complete ; several additional references may be found in the Bibliographies given by Feistmantel and other writers whose works are quoted above.]

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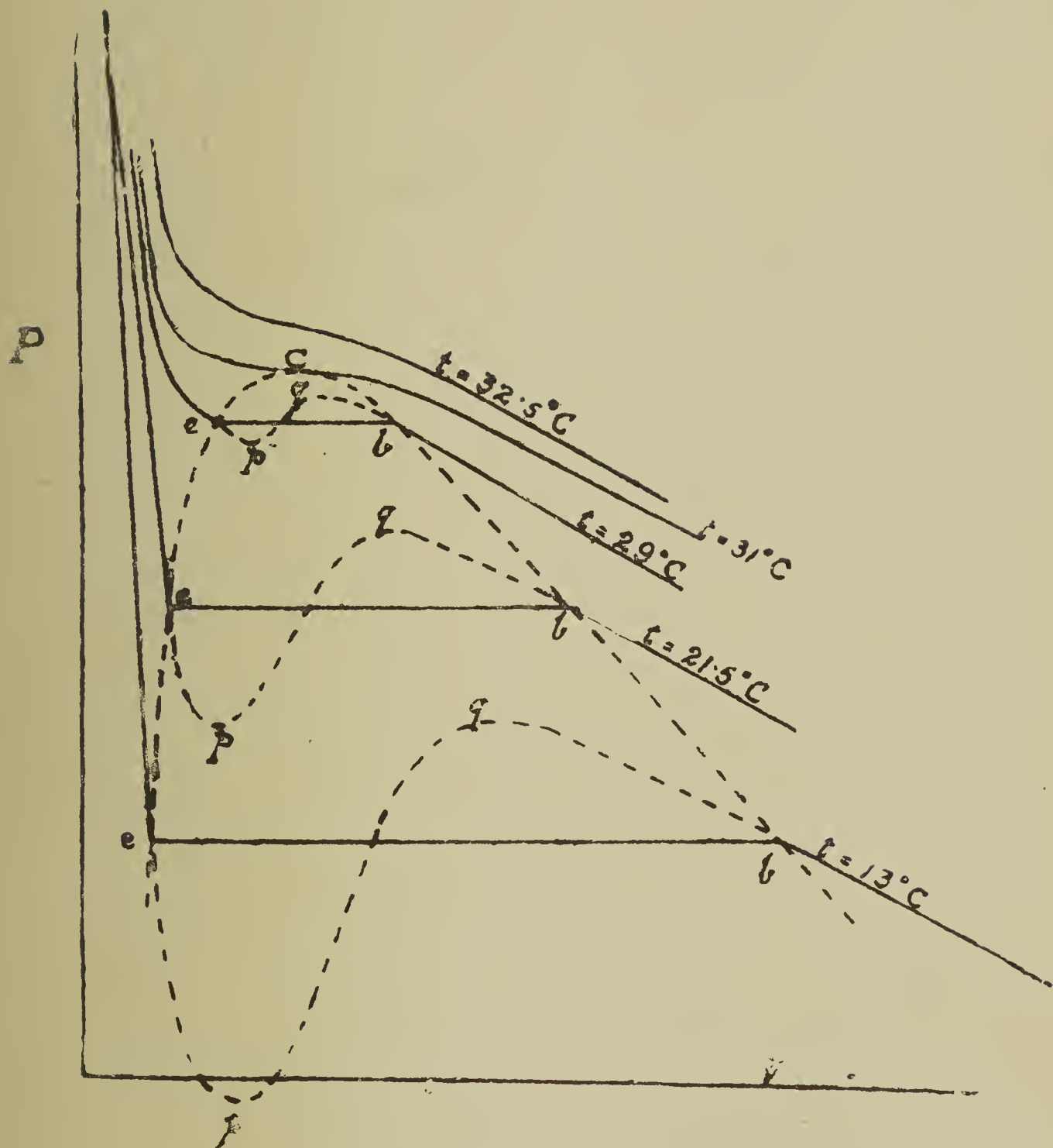
# CONDENSATION AND CRITICAL PHENOMENA.

## I. SINGLE SUBSTANCES.

THE thirty years that have elapsed since the publication of Andrews' investigation of carbonic acid have made the dogma of "the continuity of the gaseous and liquid states of matter" common property. It seems worth while to review the history of that dogma up to the present time, both from an experimental and a theoretical point of view. The phenomena established by Andrews for carbonic acid consist in the occurrence of a so-called maximum vapour-pressure increasing with temperature, and of corresponding maximum vapour-density and minimum liquid-density, which approach each other the higher the temperature, and finally coincide in a point—the critical point. These facts are all exhibited in the diagram added to his paper, wherein  $p$  and  $v$  are the two co-ordinates. The diagram accompanying this paper gives an approximate idea of Andrews' diagram for carbonic acid; the meaning of the dotted curves added to it will appear later on. The curves drawn for constant temperature, the isothermals, show a horizontal part, representing the process of condensation. A curve is drawn through the points representing the volumes of the saturated vapour and liquid curve. This is called the border-curve, or the saturation-curve, and culminates at the critical point C. The isothermals of higher temperature have a continuous course, without the sudden breaks which the lower ones show where the process of condensation begins and ends, but still showing a deviation from the shape  $pv = \text{constant}$ , consisting in a flattening in the region of the critical point.

Since then a number of other substances have been investigated in the same or a similar manner. They all display qualitatively similar phenomena; the existence of a critical point has been established for almost all substances









that could be tested, and more or less accurate determinations have been made of their critical constants, especially of the critical temperature. But though the general features of the phenomena described by Andrews have been constantly confirmed by subsequent investigations, there is a considerable amount of uncertainty as to the details of the phenomena during condensation and near the critical point. It is maintained by a number of experimenters that neither agree fully with the simple conclusions to be drawn from Andrews' diagram. In the first place the existence of a constant vapour-pressure independent of the quantities of vapour and liquid present is denied. The fact is that even Andrews himself did not find a constant condensation-pressure, but one which increased slowly during compression and somewhat more rapidly near the end of the condensation. At  $13.1^{\circ}\text{C}$ . the pressure at the beginning of the process of condensation was  $48.0$  atmospheres, and at the end  $49.5$ ; at  $21.5^{\circ}\text{C}$ . the corresponding pressures were  $58.9$  and  $61.3$ . But he ascribed this increase of pressure to the influence of a small admixture of permanent gas ( $1/500$ ). Exactly similar phenomena, essential for mixtures, as we shall see in a second article, have been observed by a number of experimenters, and some of them are bold enough to assert that impurities were out of the question in their case at least, or try to prove that the way in which the pressure increased was inconsistent with the idea that this increase should be due to impurities. Even if we knew exactly how a mixture say of ether and an unknown second substance would behave when condensed, it would still be questionable if in the experiments the equilibrium between the two phases, liquid and vapour, was always properly established, for even small admixtures occasion very marked retardation in the establishment of equilibrium. One has only to think of the slowness of diffusion under any circumstances to understand what it may come to in a long and narrow high pressure tube. Moreover, we cannot help noticing that in a few cases experiments have been made with substances that did not show any increase of vapour-pressure at all. Young and Thomas prepared

isopentane of absolutely constant vapour-pressure; the same is true for carbonic acid as prepared and investigated by Amagat. This gas contained less than  $\cdot 0004$  of gaseous impurity. The writer of this article at one time prepared a sample of carbonic acid containing something like  $\cdot 0007$  of impurity, and which showed an increase of  $\cdot 18$  atmosphere at  $15^{\circ}$  C. Comparing this result with those of Amagat and Andrews for the same substance we come to the conclusion that for carbonic acid Andrews' explanation of the anomaly was right, and that it must be due to the presence of impurities, and if so in the case of carbonic acid, why not also in the other cases? At any rate to put it as mildly as possible, we are better not to give up the simple notion of a constant vapour-pressure until it has been more conclusively proved that pure substances display phenomena that one would expect to find in mixtures.

An explanation for the alleged behaviour of pure substances during condensation was readily found. If, say, ether behaves like a mixture when condensed, why not suppose it to contain two different kinds of molecules, vapour molecules and liquid molecules, the latter probably an agglomeration of the former? Both may be present in both phases, but presumably the liquid molecules will be much more numerous in the liquid than in the vapour. Would a mixture of that kind not show an increase of pressure during compression and condensation? An affirmative answer will be found in a sentence in Van der Waals' famous treatise on the continuity of the two states. But this is evidently a slip. The difference between a mixture of liquid and vapour molecules and a mixture of two substances is that in the former the molecules can change into one another. A simple application of thermodynamics, for instance of one of Gibbs' rules of phases, shows that the process of condensation will take place at constant pressure just the same as if the molecules did not associate. If this had been remembered by the promoters of the theory, it would have led to more caution in assuming the absolute trustworthiness of experiments.

The same idea of the existence of liquid molecules as



more complicated than vapour molecules (which, by the way, is a very reasonable idea in itself) is also constantly used to explain the abnormal phenomena near the critical point. "Normal" means here again agreeing with Andrews' diagram. In heating a substance at constant volume (say in a closed tube) the liquid surface ought to disappear only when the volume is equal to the critical volume; at greater volumes the liquid ought to evaporate, at smaller volumes the vapour ought to be entirely liquefied, in both cases before the critical temperature is reached. Neither the one nor the other is true; the numerous experiments on the subject agree in some points, but differ in quite as many. The liquid surface disappears and reappears at different volumes, and the temperature is sometimes found the same always, sometimes depending on the volume. Which volume and temperature is one to choose for the critical values? And even if we knew which, how is all this to be reconciled with Andrews' conceptions? And this is not all. A number of sometimes ingenious experiments, in U tubes, O tubes and otherwise, have been devised which seem to prove that even above the temperature of disappearance of the liquid surface there is a difference between denser and lighter substance. The liquid, though not separated from the vapour, would seem still to exist and only gradually to become mixed with the vapour. The point where the meniscus disappears would not be the true critical point, but the latter would be found at a higher temperature.

There is no doubt that observations near the critical point are of the utmost difficulty, the chief reason being the enormous compressibility and expansibility of the substances in that region. It has also been proved that near the critical point exceedingly small admixtures have an enormous influence on the density. In an experiment due to Galitzine two quantities of ether, separated by a column of mercury, are enclosed in a U tube. The tube is heated above the critical temperature, and shows differences of density in the two limbs. According to Galitzine, these are due to a greater number of liquid molecules on the one side of the U tube. The writer of this article repeated this experi-

ment. The ether was purified as much as possible, but in the end the tubes appeared to contain minute quantities of gas which it is very difficult to get rid of. In one of his tubes they were estimated at  $\cdot 000086$  and  $\cdot 000026$  in the two limbs respectively (in molecules to molecules of ether). Differences as observed by Galitzine, but smaller, appeared to exist. At  $195^{\circ}$  C. (critical temperature,  $194\cdot 3^{\circ}$ ) the difference amounted to 4.5 per cent. In a second experiment a portion of the permanent gas was transported from the one limb to the other, which now appeared to contain  $\cdot 000029$  and  $\cdot 000297$  respectively. Again, a difference in density existed above the critical point at  $195^{\circ}$  C. amounting to 19 per cent., but *in the opposite direction*; while the difference in pressure was 17.5 mm. mercury in the first case and 13.1 in the second. The difference of 4 mm. is by no means sufficient to account for the difference in density, which must have been for the greater part due to the small admixture of gas which was transported from the one limb into the other. It is obvious that in an observation of the critical point in a straight tube a similar difference of density may occur, as the liquid and the gas contain different percentages of the impurity. As the process of diffusion is a very slow one, one would expect these differences to continue even though the temperature be raised above the critical point, and the phenomena that one would predict this way have a remarkable resemblance to a number of the phenomena actually observed. If the difference in density were due to a difference in the number of liquid molecules, one would expect these differences to be almost instantly equalised by the exchange and rearrangement of the particles, as this process involves no diffusion, only dissociation and association of identical particles. The presence of impurities would go a long way in explaining also the other abnormalities described above, but there is another important factor to be taken into account—*viz.*, the influence of gravitation. This influence had been overlooked until Gouy drew attention to it. It makes the density in the tube different at different levels. The density in one point may be the critical density, while in points above or below it the



density is smaller or higher. The result is that the liquid surface may disappear at any height in the tube, depending on the total volume occupied by the substance, and the critical phenomenon will not take place at one volume only, though always at the same temperature. This fact added to the influence of impurities seems to me to explain all abnormal phenomena observed, in so far as uncertain and often contradictory phenomena of that kind can be explained. The theory of the association of molecules in the liquid state seems superfluous and inadequate to explain the abnormalities.

From the above it would appear that pure observations are almost impossible to make at the critical point. In studying the more recent literature on the subject it is found, however, that the more trouble is taken to obtain pure substances the more normal the critical phenomena come out. This is, for instance, so for an interesting experiment devised by Cailletet and Colardeau. In an O tube the under half of which is filled with mercury, two unequal quantities of liquid carbonic acid are condensed in the two limbs. The mercury naturally shows a difference in level; in heating the tube to and above the critical temperature the difference does not disappear at once, and cooling the tube again gives more liquid in the limb where there was an excess of liquid before. This experiment has been repeated probably with purer gas, and the difference disappeared only quite a little above  $31^{\circ}$ , and equal quantities condensed at the two sides in cooling. The presence of some impurity in the liquid or gaseous  $\text{CO}_2$  explains the former result readily. Even in cases where impurities have not been entirely removed (and that would be in 99 out of 100) very trustworthy experiments may be obtained by thoroughly stirring the substance. A little iron rod moved up and down in the tube by a strong electro-magnet outside serves the purpose admirably and is astonishingly effective. The equilibrium between the two phases, which, according to some very interesting time experiments of Gouy, would take days to establish itself, only takes a few moments when the stirrer is set in action; a result at once

explicable on the impurity-diffusion theory developed above. The critical phenomena become very simple, and in accordance with theory, even for gases in which the presence of some impurity is revealed by a not quite constant vapour-pressure. The temperature at which the liquid-surface disappears is found independent of the volume and is therefore easily ascertained; the best method is to apply a slowly rising and falling temperature alternately. If we assume the critical isothermal between certain limits to have a similar shape on both sides of the critical point, the true critical density will be found by calculating the average density when the liquid surface disappears half way up the column. Very concordant values for the critical density are found by this method, and I believe that the optical method (if thus applied) does not deserve all the severe things that have been said about it. There is only one point that leaves some uncertainty in the method; one or two tenths of a degree above the critical temperature a very characteristic blue mist fills the tube, probably due to liquid particles floating in the substance. But in his best experiments the writer of this article saw this mist disappear at less than  $\cdot 2$  above the critical temperature as measured by the disappearing of the liquid surface, and the uncertainty is therefore very small indeed. If no sudden changes of volume or temperature take place all the other critical phenomena, like the striæ described by Andrews, hardly show themselves, if they do so at all.

There are other methods for determining the critical constants. Chappuis, for instance, measured the refractive index of the two phases by an interference method, and calls critical temperature the temperature where the two coincide. But if impurities are present, and retardation in the process of mixing, the refractive indices will not be equalised at the critical temperature, and the method is bound to give a result which is too high. For carbonic acid he found  $31\cdot6^{\circ}$  C. (Andrews  $30\cdot90^{\circ}$ , Amagat  $31\cdot35^{\circ}$ ). Amagat determined the critical temperature of  $\text{CO}_2$  by plotting the densities as far as possible and completing the curve. A direct method would seem preferable, though in the hands



of an experimenter like Amagat the method no doubt yielded a very accurate value. The direct method described above gave the writer of this article  $31.2^{\circ}$  C. for  $\text{CO}_2$  containing about  $\cdot 0007$ , a very small difference to be sure.

The critical volume is now generally obtained by a graphical method depending on a law discovered by Cailletet and Matthias, that "the mean of the vapour and liquid densities is a linear function of the temperature". Where this line cuts the border-line of densities the critical density is found. The law holds very well where it has been tested (for instance, for  $\text{CO}_2$ , Amagat; isopentane, Young and Thomas, etc.). [Certain exceptions will be referred to in the sequel.] From a minute study of the best results obtained, one would conclude that the line is not perfectly straight, and therefore the law only approximate after all. This is of importance because it suggests the question in how far one is entitled to use it for determining the critical density. There are other cases in which empirical laws which hold perfectly at some distance from the critical point begin to fail near the critical point. The height of a liquid in a capillary tube is a linear function of the temperature, until close by the critical temperature, when a marked curvature in the line appears. It is, however, questionable if the determination of the critical density (even if made according to the principles laid down above) will ever be accurate enough to discover a small deviation in the "diameter" near the critical point, if there is any. But it will have to be tried. There are certain groups of bodies which do not obey the law of the diameter, but yield a line with very marked curvature. These bodies, such as the fatty acids, the normal alcohols, water, curiously enough are the same as disobey most of the other laws that hold for other substances. This exceptional behaviour is ascribed to a conglomeration of molecules to groups chiefly at the higher densities; a similar association of molecules would not take place for the majority of substances which follow the general laws.<sup>1</sup> A very satisfactory justification of this explanation

<sup>1</sup> Compare an article by Dr. J. Shields in "SCIENCE PROGRESS," pp. 265-278, December, 1894.

will be discussed presently, and the theory of the association of molecules to groups for those substances will then appear a very probable one. But it must once more be pointed out that an association of this kind would never be able to explain a change in the vapour-pressure, as has been attempted by Batelli and others. This was already discussed above.

The problem of the behaviour of molecules in the different states of matter belongs to the kinetic theory of matter, a theory which had been worked out for gases long before Andrews published his investigation on the condensation and critical phenomena of  $\text{CO}_2$ . It was Van der Waals who succeeded in drawing Andrews' results within the range of the kinetic theory, and at the same time expanded the idea of the continuity of the two states. It was suggested by James Thomson that the isothermal does not really possess the two sharp breaks at the beginning and at the end of the condensation, but that the two parts of the curve outside the border-curve are to be joined by a curve with a maximum and a minimum like a wave-crest and a wave-trough. Three of such curves are given in the diagram. The reality of the phases between  $e$  and  $p$  is shown by the possibility of lowering the pressure of a liquid a good deal below its vapour-pressure as long as no vapour is present. The phases on the crest part ( $b$   $g$ ) have not been realised in the same way. But both these and the phases between  $e$  and  $p$  occur where liquid and vapour are separated by a curved surface. All this makes the existence of the rest of the hypothetical curve more or less probable also. As early as 1873, Van der Waals published his famous memoir in which he proves that the kinetic theory leads to an equation for the isothermal having the shape proposed by Thomson.

The equation is  $\left(p + \frac{a}{v^2}\right) (v - b) = R (1 + a t)$ . This result he obtains by assigning a finite size to the molecules and attractive forces between them acting over distances large compared with the distances of neighbouring molecules. The term in  $b$  depends on the former, the term in  $a$  on the latter supposition. By increasing  $t$  in the formula



the wave-shape of the curve gradually disappears, and above a certain temperature has vanished altogether. The point in which the wave disappears as it were has all the properties of Andrews' critical point. In fact qualitatively Andrews and Van der Waals' diagrams are exactly alike, at least outside the border-curve. Inside the curve the theoretical isothermal has the wave shape as described with points between  $p$  and  $q$  in which the condition of the substance is essentially unstable.  $\left(\frac{dp}{dv} > 0\right)$  Experiment shows that the substance divides itself into two portions, both stable and also in equilibrium with each other, an equilibrium which is independent of the qualities of the two "phases" present, the pressure depending on the temperature only. The kinetic theory is not able to determine, in a general way, the condition of equilibrium, and in that way find points belonging to the border-curve. Too little is known of the nature of the superficial layer between liquid and vapour. In cases of this kind we take refuge in thermodynamics. The criterion to which it leads in this case was found by Maxwell, and afterwards by Clausius, and may be stated thus: the horizontal line which connects the two co-existing phases on the isothermal encloses with the wave-crest and the wave-trough surfaces of equal area. By this rule it is possible to determine the vapour-pressure, and the vapour and liquid density from the theoretical isothermal. But no more than other rules arrived at by thermodynamical considerations does it give us an insight into the mechanism on which the equilibrium of the two phases depends. Kinetically the condition of equilibrium is this: that the same number of molecules passes from one phase into the other, as backwards; but, as was said before, this condition cannot be applied unless by making special assumptions about the nature of the bounding surface, which impairs the generality of the result obtained.

Quite lately, a most interesting theory was published by Prof. Van der Waals regarding capillary phenomena, in which he imagines the surface layer between the phases to contain all the phases on the theoretical isothermal between

the liquid and vapour, in the order in which they lie on the isothermal. It is impossible to explain here how the condition of equilibrium is arrived at. Suffice it to say that the theory is thermodynamical. Though among these phases there is a group of phases necessarily unstable when supposed to exist over a finite space, Van der Waals proves that the layer as conceived by him, in which each of the phases exists over an infinitely small distance, is stable as a whole. According to this theory the continuity of the two states within the border-curve would not only be an imaginary, a theoretical one, but a real one, and in a seemingly discontinuous surface between two phases we should have a special kind of continuous transition. This is the widest possible generalisation of the dogma of the continuity of the two states. The more one considers the matter the more one is struck by the beauty of the theory, and the remarkable simplicity of the conception of the continuity which it contains.

The application of the theory to a curved surface leads to some interesting results. The condensation-pressure appears to be different in that case to what it is at a plane surface, a fact which a direct application of thermodynamics had already revealed. The pressure is higher in one of the phases than in the other, and both differ from the ordinary condensation-pressure given by the height of the straight lines in Andrews' diagram, being either both higher or both lower.

It is also found that possibly a continuous transition exists above a certain temperature only, below which the transition would have to be discontinuous; and a number of other things as well. The theory leads to a law giving the change of the capillary constant  $\sigma$  with temperature  $t$  near the critical temperature  $t_c$ , *viz.*,  $\sigma = c \left(1 - \frac{t}{t_c}\right)^m$  in which  $c$  is a constant and  $m$  would be  $1\frac{1}{2}$  close to the critical point. This law was tested with the experimental results obtained by De Vries and Ramsay and Shields; it appears that at some distance from the critical temperature  $m$  is a constant quantity, but smaller than  $1\frac{1}{2}$ , about 1.25 for most substances. The only exceptions are the same substances



that were mentioned before as disobeying the law of the diameter, and for which an association of molecules is assumed. The capillary constants obtained for these bodies allow of a calculation of the amount of association by means of the law of corresponding states, a law which will be considered later on. This will be explained in Dr. Shields' article quoted above.

The law could not be tested up to the critical point as the experiments did not go far enough. Verschaffelt has measured the constant for carbonic acid up to  $30^{\circ}$  C. and finds that  $m$  is higher than 1.25 near the critical point. But his results depend greatly on Amagat's values for the densities of  $\text{CO}_2$  near the critical point, which at temperatures near the critical point were found by graphical interpolation from observations at lower temperatures; this method unhappily leaves uncertainties which make a decision between 1.5 and, say, 1.3 impossible. Suppose, however, the law  $\sigma = c \left(1 - \frac{t}{t_c}\right)^{1.5}$  was not confirmed, this would not show that the idea of continuity in the surface-layer ought to be given up. The way in which the formula is arrived at seems to show that it depends on Van der Waals' equation of condition mentioned before, which, though of great importance, has been shown not to agree numerically with observed facts.

The difference between the formula  $\left(p + \frac{a}{v^2}\right) (v - b) = R t$  and observation is too absolute to be treated as a mere correction. In fact, though at the time it was impossible to say in how far the formula would agree with facts, one thing was pointed out by Van der Waals himself, *viz.*, that the formula would certainly not hold beyond certain densities. Its applicability has since been proved to be even smaller than was anticipated and might have been expected after the successful calculations with regard to carbonic acid. For one thing, it leads to a value for the critical volume  $v_c = 3 b = (\text{approximately}) \frac{3 t_c}{8 + 273 p_c}$  which relation has never been confirmed,  $v_c$  always being a great deal less than

its value, calculated from  $p_c$  and  $t_c$ , mostly about  $\frac{2}{3}$ . Again, the critical volume should be 2.667 times less than the volume calculated according to Boyle's law, while it has been found to be 3.7 or 3.8 times smaller. Apparently even at the critical point Van der Waals' equation does not hold. It seems as if the changes in density on the isothermal are much more sudden than according to Van der Waals' formula, and as if the process of transition from vapour to liquid is connected with a more intimate combination of the particles. Attempts have been made to improve upon Van der Waals' formula by starting from more general suppositions about the molecular actions, both at a distance and during collision. Formulæ with more than two constants are obtained that way which can be made to agree with facts over a larger area of the diagram. Those formulæ are mostly half empirical and are nothing more than Van der Waals' formula with a few more judiciously introduced constants. Professor Tait arrives at a formula containing four constants, the physical meaning of which is well defined; but even this formula does not yield satisfactory results. The value of the critical constants is derived from the formula in the way originated by Van der Waals; but in order to make the formula agree with Amagat's results for carbonic acid it appears necessary to calculate two systems of constants based on two different values for the critical volume, one set for the observations at higher and the other set for observations at lower density. Even then the agreement is not perfect. Professor Tait justifies this doubling of his constants by the fact that experiments show the critical volume to lie between two limits. But it was shown above what this apparent range of critical volumes was due to, *viz.*, the action of gravitation. At the same time, even if the critical isothermal was very nearly horizontal and straight in the critical point, how can  $v_c$ , the volume in the summit of the border-curve, by the way in which it is derived from the formula possibly have two values or a range of values? It seems, therefore, that even Professor Tait's formula with its four constants is not capable of describing the behaviour of carbonic acid. And



though one or other of the formulæ mentioned may occasionally be used with success, the problem of a satisfactory formula does not seem much nearer its solution than where it was left by Van der Waals in 1873. There is one law, however, essentially empirical, which has been found pretty well confirmed where tested, *viz.*, that the pressure at constant volume is a linear function of the temperature. The accurate series of observations due to Amagat, Ramsay and Young, etc., confirm this law, though the most recent results obtained for isopentane and hexane by Young and Thomas, and for a number of liquids by Barus and especially Amagat, show slight but certain deviations. Van der Waals' formula is in form a special case of this law, but theoretically there is nothing to say in favour of the general one.

While it is at present impossible to explain the behaviour of a substance in detail on the kinetic theory, a remarkable set of laws has been discovered which shows the existence of a great resemblance between the behaviour of different substances, the laws of corresponding states of matter. The law was deduced by Van der Waals in 1880 from his formula, but appears to hold in circumstances where the formula itself would not be applicable at all. This is quite intelligible, as the law would follow from a good many equations different from Van der Waals' equation. In fact, as was first pointed out by Kamerlingh Onnes in 1881, it follows from a general hypothesis, *viz.*, that the molecules of different substances are similar bodies of constant dimensions acting upon each other with attractive forces that can be reduced to a surface pressure, or forces inversely proportional to a certain power of the molecules. In both cases by the application of Newton's principle of the dynamical similarity the law of corresponding states of matter is arrived at. The simplest way in which to put the law is that if  $p$ ,  $v$  and  $t$  are expressed in terms of their values at the critical point, the relation between them is the same for all substances. This law leads to numerous consequences which may be used in testing it, a few important ones of which I will here mention. In the first place, that there must be a relation between the three

critical constants, so that say  $v_c$  may be found from  $p_c$  and  $t_c$ ; also that  $v_c$  should be in a constant ratio to the volume as calculated by the laws of Boyle and Charles. These two relations were mentioned above, and we saw how they are confirmed by experiment. Another consequence of the law is that the vapour-pressure expressed in terms of the critical pressure will be the same for all substances at temperatures which are the same fractions of the critical temperature. Similar relations regarding the densities of vapour and liquid, and even quantities like the capillary constants, co-efficients of viscosity, co-efficients of expansion, etc., may be derived from the general law. It is difficult within the scope of this article to give an idea in how far experiment confirms these laws. Sometimes the agreement is very close, in others it is less satisfactory, but for most substances at least approximate even for pretty high densities. Again, the acids, alcohols, water, etc., the groups of bodies that were mentioned before as disobeying other laws of liquids, form exceptions. It will be better understood now what right we have to explain the abnormal behaviour of those bodies by association of molecules. If we assume that for the majority of substances no such association takes place, substances in which it does cannot be regarded as dynamically similar, and for them the law cannot therefore hold.

These laws in so far as they are confirmed restrict the number of isothermal equations that are possible. When in the isothermal equation we introduce the critical constants as far as possible, all constants like  $a$  and  $b$  in Van der Waals' equation, in other words, everything specific for the special substance, should disappear. An equation in which that does not happen is in contradiction to the law of corresponding states. On the other hand the hypothesis on which the law may be based shows that there are quite a number of equations to be imagined which could be in agreement with the law.

Finally, therefore, we are confronted with the fact, that though important laws both empirical and semi-theoretical have been discovered, a satisfactory equation between  $p$ ,  $v$ ,  $T$



does not exist. Perhaps the problem to find one which would embrace the whole field of possible values for  $p$ ,  $v$ ,  $T$  is insoluble, but the dogma of the continuity as founded by Andrews and enlarged by Van der Waals seems independent of this equation. If we take Andrews' diagram and complete it inside the border-curve in the manner of Thomson and Van der Waals, we have the whole dogma before us. The conditions outside the border-curve are to be realised by experiment, those inside only under special conditions or in the surface layer between the two phases. The reality of the isothermal inside the border-curve is hypothetical, but so acceptable that at present in similar cases of co-existence of phases the existence of a theoretical continuous transition between the phases is invariably admitted. We might almost say that thermodynamics is essentially dependent on hypotheses of that kind.

In the light of the dogma it is easily seen that a difference between liquid and vapour or gas does not exist. In fact this point was made entirely clear by Andrews himself. It is, however, not unnecessary to lay some stress on this point, as even now there seems to be a tendency in the minds of physicists to define gas-vapour and liquid in a way that shows that the bearing of the continuity is not sufficiently understood. Very generally one finds a substance called a gas (or a true gas) above the critical temperature and vapour (or liquid) below the critical temperature. This will do as a conventional distinction, but there is no real foundation for it. One might just as well call a substance a gas above the critical pressure and a vapour (or liquid) beneath it. The critical constants have a special meaning *in the critical point only*, and the critical isothermal is no line of demarcation between different conditions or properties of the substance.

In a second article the condensation and critical phenomena of mixtures will be considered, to which we have been led up naturally in discussing the experiments on so-called pure substances.

J. P. KUENEN.

## THE ORIGIN OF LAKES.

THE study of lakes has recently attracted so much attention that Limnology is now recognised as a special branch of geography, and a large number of problems connected with lakes are being solved. The one which has been of the greatest interest to geologists is without doubt that of the origin of the hollows in which lakes are contained, and although the existence of a large number of these hollows has been satisfactorily explained, there are many others whose origin is still uncertain. As the subject is one which may well occupy the attention of local observers, no apology is needed for attempting to show the position in which we now stand as regards our knowledge of the origin of lakes.

General interest in the question of the formation of lake basins was undoubtedly aroused in the first place as the result of the late Sir Andrew Ramsay's paper "On the Glacial Origin of Certain Lakes in Switzerland," etc., published in 1862 (1), in which he ably advocated the formation of rock basins by glacial erosion, but his views are so well known that it is only necessary to allude to this paper as the starting-point of modern work on lake formation. Since that time a host of observers have paid attention to the physical structure of lake basins, and we now have accurate surveys of a large number of lakes, notably those made by Mill in England and by Delabecque in France. As the result of this work, the subaqueous scenery of lakes is in many cases as well known to us as that above water, and we are consequently able to apply our knowledge of the mode of operation of different agents of erosion with greater certainty than could be done before the execution of these surveys.

Though the term "rock" is applied by geologists in most cases to aggregates of mineral without reference to the compactness or coherence of the component particles, its



use in a somewhat different sense in the case of lakes is not likely to give rise to any confusion, and there is no objection to adopting the usual classification of lakes into two divisions, namely, the lakes which are contained in rock basins, and those which are not, though perhaps a four-fold division would be more useful, the lakes being classified according as they occur (i.) in craters, (ii.) in depressions which have been blocked up by some material, (iii.) in areas which have been depressed by earth movement, and (iv.) in hollows of erosion; this latter classification I propose to use in the present paper.<sup>1</sup>

(i.) *Crater lakes*.—The existence of lakes occupying the site of volcanic craters has long been known, and their origin is quite apparent. Many crater-shaped hollows are ready to receive water, after the cessation of volcanic action; the Lucrine Lake and Avernus are classical examples of lakes formed in this manner. Several crater lakes of the volcanic region of Central France have been sounded by M. André Delabecque, and their symmetrical shape and considerable depth shown (2). Lac d'Issarlès in the department of Ardèche has a depth of 108 metres, Lac Pavin of 92 metres, Lac de Tazanat of 66 metres, and Lac Chauvet of 63 metres. The three last-mentioned lakes are in the department of Puy de Dôme, and their boundaries and subaqueous contours are remarkably circular. Concerning Lac d'Issarlès, Scrope writes that it is one of those lakes which “differ from ordinary craters, not only in their greater dimensions, but in the nature also and disposition of their enclosure, which is usually of primary, or, at all events, pre-existing rocks, merely sprinkled more or less copiously with scoriæ and puzzolana, little if at all elevated above the surface of the surrounding country”; it thus becomes clear that crater lakes may lie in hollows formed by explosion or by accumulation of volcanic ejectamenta, or by a combination of the two processes.

<sup>1</sup> I had written this article before reading the admirable chapter upon lakes in the second edition of Sir John Lubbock's *Scenery of Switzerland*, where a similar classification is proposed. I hope all who are interested in the question of lake-formation will refer to that work.

(ii.) *Lakes in depressions which have been blocked by some material.*—The variety of materials which by damming up valleys give rise to lakes is very great, and a much larger proportion of lakes than is commonly supposed probably owe their existence to the formation of a dam across a valley. In the case of such blocked valleys, the water which accumulates behind the dam to form a lake may eventually find its way over the dam, and if this be composed of incoherent material, as frequently occurs, the dam is readily worn away and the lake is a short-lived one and is rapidly drained, its position being often marked by a peat-bog, overlying the deposits which were laid down on its floor prior to its destruction. The number of peat-bogs occurring behind dams, as compared with existing lakes in such a region as that of the English Lake District, proves that the surviving lakes are a mere fraction of those which once existed. But other dammed-up valleys are blocked by dams, of which the lowest point is at a higher level than that of a col uniting the valley with an adjoining one, in which case the lake fills up to the level of this col and drains through it, oftentimes over solid rock; lakes of this character are much more durable than those which discharge over incoherent dams, and are likely to survive when the latter are destroyed. I have elsewhere attempted to prove that a large number of the tarns and lakes of English Lakeland were formed in this way, and that their formation was coincident with deviations of the drainage system, often of considerable importance (3).

Passing on to consider the various kinds of dam which give rise to lakes, we may notice in the first place lakes held up by ice, whether in the form of an ice avalanche or a glacier. The lakes formed by ice avalanches are necessarily of an ephemeral character and are mainly interesting on account of the damage wrought by floods when they burst. The best known instance of a lake of this character is that of the sheet of water produced by the blocking up of the Dranse by the Gétroz Glacier, which caused the disastrous flood in Rhone Valley in 1818. Of glacier-dammed lakes, the Märijelen See is too well known to require more



than passing notice; but magnificent examples occur in Greenland, and in some of these the water drains over or under the ice, whilst in others the outflow resembles that from the Swiss lake in being over solid rock. Some interesting lakes of this character are figured in Plates A and C of the first part of the *Meddelelser om Grönland*. I need only refer here to the famous Parallel Roads of Glenroy and the great terraces of "Lake Agassiz" in North America, which are considered to be due to glacial dams of this nature.

In the lowland tracts of river-basins crescentic lakes often result from the formation of "cuts-off," the former sinuosities of the river being barred by river-deposit and giving rise to lakes. Good examples of these are found in the lower reaches of the Mississippi and are described in the nineteenth chapter of Lyell's *Principles*. Accumulations of vegetable matter are frequently sufficient to obstruct the drainage of streams to so great an extent as to form lakes, which are subsequently converted into peat-mosses. Sir A. Geikie records the formation of lakes in North America which have covered thousands of acres and which were due to the formation of a dam of vegetable matter produced by beavers cutting down trees.

Blown sand is another material which is competent to form a barrier enclosing a large sheet of water. The well-known *étangs* in the neighbourhood of Arcachon were formed by the gradual advance of sand-dunes from the ocean, converting bays into inland pools, the surfaces of which are frequently at a considerable height above the ocean level.

In upland districts numerous tarns and lakes are blocked up by barriers formed of landslip material, screes, dry deltas, snow-slope detritus and glacial accumulations. A good example of a lake formed by landslips is that produced near Terranuova during the Calabrian earthquake of 1783. Examples of the other barriers are furnished by various tarns in the Lake District. Goatswater, near Coniston, is blocked by screes; Smallwater, near Haweswater, by snow-slope detritus; several of the tarns by glacial accumulations,

especially the moraines of combe-glaciers, whilst Sty Head Tarn is a good example of a lakelet due to the formation of a dry delta, formed by a stream descending from the two Gables. The freshness of the surface of one bank of the stream, where much material has evidently fallen in, indicates that the formation of this tarn may have been quite a recent event, and it would be interesting to know whether there is any proof of its non-existence in historic times. It is evidently becoming filled up very rapidly by the deltas of the streams which flow into it, and this also indicates a recent origin. Although several of the lakeland tarns have exits flowing over the barrier, the larger proportion of them drain over solid rock, and naturally several of these occur amongst the shallow valleys of the upland plateaux where cols lower than the drift-barriers frequently existed. The tarn at Watendlath, if drift-dammed, requires the filling in of a very deep cañon-like gorge, whose depth must have been much greater than its width at the top; if the evidence for the formation of the other tarns of Lakeland by drift-dams were not so strong, one would feel inclined to admit that Watendlath Tarn lay in a true rock-basin, but it is hardly likely that this tarn had a special origin, and after re-examining the surroundings I am persuaded that the drift-filled gorge did exist. This would necessitate the beheading of the old Lowdore-Watendlath Valley in pre-glacial times by a ravine cutting back from Rosthwaite which became filled with drift in the glacial period. It is very desirable that some similar case in a less picturesque area should be investigated by boring, for if narrow ravines were common in pre-glacial times, a great many apparent rock-basins may have narrow, sinuous, drift-filled gorges, which might easily escape detection. The comparative absence of narrow gorges in our upland regions is a somewhat surprising fact, and I am inclined to think that the true explanation is that a large number of them, which existed in preglacial times, have been filled up and completely concealed by drift accumulations. Under the heading of lakes in depressions which have been blocked by some material may be included those lakelets which lie



solely in hollows in drift, the barrier in this case extending all around the lake. The name "kettle-holes" has been applied to lakelets of this character by some American geologists, but the late Dr. Carvill Lewis, who gave a good account of them, spoke of them as morainic meres. Good examples occur "at Ellesmere in Cheshire. At this picturesque locality most of the meres—over twenty-five in number—have received separate names all ending in 'mere'" (4).

Turning now to larger lakes, which are due to barriers of drift, I have given reasons for believing that the principal lakes of English Lakeland are also due to the blocking of valleys by barriers of drift, and that they do not occur in rock-basins. These lakes have frequently been sounded, most of them in considerable detail by the late Mr. Clifton Ward whose work on the Lake District was one of the most substantial contributions to the geology of that region (5), but especially by Dr. H. R. Mill (6) whose valuable paper has given us a true insight into the character of the subaqueous scenery of these lakes. It is clear, from perusal of Dr. Mill's work, that the subaqueous features of the lakes do not differ in any essential particular from the subaerial features of the adjoining valleys, and that subaqueous and subaerial features alike have been produced by the same agents of erosion; the character of the scenery in each case forbids the supposition that it has been produced by glacial erosion, and we find plenty of evidence that glacial erosion has merely given a finishing touch to the work of the other subaerial agents. We must, therefore, attribute the formation of these lakes to earth-movement or blocking of valleys by drift accumulations, and I have given reasons, after study of the distribution of the drift and of the anomalous courses of many of the rivers of Lakeland, for attributing the formation of the lakes to the latter cause. Some of the lakes, such as Ullswater and Haweswater, appear to drain over the drift-barrier, but the greater number, including Windermere, Bassenthwaite, Thirlmere and others, have the drift-filled valleys occupied by insignificant runnels,

whilst the lake is drained through a rock gorge, whose head once formed a col at a lower level than that of the drift barrier. A similar instance of the formation of lakes, accompanied by a marked deflection of drainage, has been described by M. Delabecque in the case of Lakes Longemer and Gérardmer in the Vosges district (7). This method of formation of lakes was described in 1894 by the late Professor Carvill Lewis, in the work already cited. He states that "if the moraine is compact, an outlet for the lake is often cut through the rock, and a post-glacial gorge is formed". He gives Lake Constance as an example, and observes that "this lake is dammed on its north side by the great terminal moraine of the Rhine glacier, and owes its large size to the flatness of the region in which it lies. Its present outlet to the west by way of Schaffhausen, is a post-glacial one cut through rock. Before it was obstructed by the moraine, the pre-glacial Rhine flowed northward into the Danube." Lakes blocked by moraines, whether the outlet is now over the moraine or over solid rock, are spoken of by Professor Carvill Lewis as "inter-morainic lakes".

Before quitting the class of lakes produced by the formation of a dam across a valley, allusion must be made to those due to a lava-flow obstructing the drainage of a valley, as happened in the case of the lava-flow descending from Etna in 1603, which blocked the valley of the Simeto. Lakes must frequently have been produced in this manner in volcanic regions.

(iii.) *Lakes in areas which have been depressed by earth-movement.*—Differential movement of portions of the earth's crust has long been known to have produced lake-basins both in volcanic and non-volcanic regions. A good example of a lake of this character in an old volcanic region is Lake Balaton (the Platten See) in Hungary, which has been described by Professor Judd (8), and the instances described by Dr. Gregory along the "Great Rift Valley" of Africa are now familiar to all readers (9). The proofs of the formation of lakes by earth-movement are particularly clear in the case of the ancient lakes Bonneville and Lahon-



tan in the western territories of North America, for the deformation of the terraces has been worked out in the case of those lakes, and some of the terraces are actually seen to be cut by fault planes (10). Dr. Gilbert, who described the geology of Lake Bonneville, has also detected proofs of differential movement amongst the old terraces of Lake Ontario, and a number of papers have been published by Dr. J. W. Spencer, giving accounts of his detailed work on the "warping" or deformation of the terraces around several of the large Canadian lakes of the St. Lawrence Valley, one of which appears in the *Journal of the London Geological Society* (11). It may be observed here, that although there is evidence of considerable earth-movement having affected the British area since the formation of the principal British lakes, it is doubtful whether any of these lakes owe their origin wholly or in part to this earth-movement, which appears to have been singularly uniform in amount over very wide areas, and therefore to differ from the "warping" movements which have taken place in Canada and the Western Territories. Still it is possible that differential movement has played some part in the formation of some of our lakes, but it will require much more work upon the physical structure of our lake-basins before the partial or entire production of any of them by differential movement can be established or disproved.

There is one kind of earth-movement due to local causes which must be noticed, as some lake-basins are undoubtedly produced thereby. I refer to the solution of material underground and the consequent subsidence of overlying rocks. The artificial removal of salt in the New Red Sandstone areas of North-west England and the consequent subsidence of the ground is well known to all, and the removal of limestone may have given rise to some of the smaller lakes that occur in limestone regions in Britain, owing to the falling-in of the roofs of cavernous hollows underground. The Königsee has been cited by Credner as a lake which was probably formed by the removal of soluble matter from beneath it; and many other instances probably occur.

(iv.) *Lakes lying in hollows of erosion.*—The formation of rock-basins by erosion is a question which has given rise to a great deal of controversy, and the origin of rock-basins by erosion is still to a large extent enveloped in mystery. There are many lakes, apparently rock-basins, which lie in hollows so diminutive that no one would invoke the action of differential movement to account for their formation, and should their existence as true rock-basins be established they must be admitted to have been produced by erosion, though it by no means follows that the agent of erosion must necessarily have been ice. In our own country Mr. Watts has claimed the lower lakelet in the hollow of Cwm Glas in Snowdon as “certainly confined in a rock-basin, as rock occurs at its actual outlet and at every point where any former outlet might have been possible”(12). M. Delabecque, in the paper on the lakes of the Vosges district to which I have already referred, describes a lakelet of some size (L. Retournemer) which the geological map indicates as being barred by moraine, but states that to him it appears to be entirely situate within rock *in situ*, and that it must be grouped amongst the rock-basins of which the origin is still but little explained. The work of M. Delabecque is evidently marked by much care, and he has paid such special attention to lakes with particular reference to their existence in rock-basins that he is hardly likely to have overlooked any drift-filled depression to which this lakelet may be due. Mr. H. P. Cushing (13) describes diminutive lakes on the tops of low hills bordering the Muir Glacier of Alaska. Several are situated on nunataks near the end of the glacier and occupy small depressions or basins on the tops of ridges; they are only a few yards in diameter and of no great depth. “Some of them clearly occupy rock-basins, rock in place being readily traced all round them . . . other lakes have a portion of their shores formed by glacial debris. . . . That the glacier has done little more than to remove the loosened rock and polish the resulting surface is shown in a vast number of localities. . . . All these basins which I saw lie in small valleys on the mountain tops, whose presence seemed to depend on the fissure systems and on the varying depths



to which loosening of blocks had taken place." The formation of these little rock-basins, then, appears to have been primarily due to unequal weathering, the sole work of the glacier having been to remove the weathered blocks.

During the present year I had an opportunity of seeing some very tiny pools produced by unequal weathering in a way which, if conducted on a larger scale, might give rise to small lakelets. In the Langstrath Valley of the English Lake District is an alluvial plain, terminated by a gorge which I have elsewhere described as apparently due to the stream issuing from a vanished lake. A wall runs at right angles to the gorge on the east side. On the south side of the wall some exquisite potholes are seen at a considerable distance above the stream, though these are not the rock-basins to which I wish to refer. On the north side of the wall are shallow depressions in the rock, in various stages of formation. One, eighteen inches long and three inches deep, was filled with water, but it had a deposit of peaty silt on its floor. Another "basin" about three feet long was filled with heather, grass and moss, and a similar patch of moss, grass and heather occupied a space about twelve feet long, surrounded on all sides by naked rock. It is well known that the organic acids supplied by vegetation assist the weathering of rock, and that the water is also held against the rock for a much longer period where the rock is covered by vegetation than where bare, so that vegetation tends to cause the rock to be etched away beneath it, and in this Langstrath rock one saw how small lakelets might be produced, and indeed were in actual process of formation on flattish surfaces of rock owing to this cause. It is doubtful how large a basin could be produced in this way, but I see no reason why considerable lakelets should not arise in this manner after the death of the vegetation which had covered the rock. It is well known that peat-mosses are frequently due to the former existence of lakes, but it is not so generally recognised that, conversely, lakelets may be due to the former existence of peat-mosses.

I have been induced to write this paper on lakes because I believe that there is still much valuable work to be accomplished even in our country with reference to the origin of

lakes. We have lakes of many kinds—the fenland meres, the Norfolk Broads, the kettle-holes of our drift-covered lowlands, the valley lakes of upland regions and the gloomy tarns of the mountain recesses—all differing from one another in many characteristics, but broadly grouped together under the one heading, “lake”. Because some of these have been accounted for, it by no means follows that the origin of all has been explained, and the student of physical geography may well be occupied for many years to come in working out problems connected with the Limnology of the British Isles.

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## THE CAUSES OF VARIATION,

IN the last few years an ever-increasing amount of attention has been given to the study of the facts of variation, for it has gradually become more and more evident that this forms one of the most important vantage grounds from which the problems of evolution may be attacked. The importance of this study depends not a little on the consideration that it is based upon the collection and determination of sure and solid facts, which do not depend for their veracity upon the validity of any particular hypothesis or theoretical consideration. Even more interesting, in many ways, than the study of the *facts* of variation is that of the *causes* of variation. To what are the differences in form and structure, often by no means slight, which individuals of a species show among themselves, due? Why is it that offspring do not bear an exact resemblance to the physical form of their parents?

Into this question of the causes of variation, Darwin, who was the first to show the vital importance of the study of the facts of variation with reference to the problems of evolution, entered but little. He considered that variation "is generally related to the conditions of life to which each species has been exposed during several successive generations," and that "changed conditions act in two ways, directly on the whole organisation, or on certain parts alone, and indirectly through the reproductive system" (1). Another view which has been frequently upheld, especially by certain American scientists, is that variation is the result of an inherent tendency on the part of the organism to vary. More recently it has been shown that the problem of the causes of variation is intimately bound up with the question of sex, for the characters of offspring are produced by a mingling of those of their parents, and this mingling may not be in fixed and exactly similar proportions. Thus Wallace believes diversity of sex to be of primary importance as the cause of variation (3). Weismann also is con-

vinced that conjugation in unicellular and sexual reproduction in multicellular organisms are the means of producing variation (4). But the ultimate cause of hereditary variations he considers to be due to the constant recurrence of slight inequalities of nutrition in the germ plasm, or reproductive substance of the organism. Weismann also considers that variation depends upon the action of environment, but as he does not believe that variations so produced can be transmitted to the next generation, he is compelled to adopt the hypothesis mentioned. His views are best illustrated by a concrete example, the case of twins in the human race. As a rule, twins differ from each other in mental and physical characteristics just as much as do children of the same parents born consecutively. Occasionally, however, the twins show so close a resemblance that they cannot be distinguished from each other by strangers. These may be called "identical" twins, and the former "dissimilar" twins. In all probability dissimilar twins are derived from two ova, which have of course been fertilised by two different spermatozoa, whilst "identical" twins are derived from a single ovum and spermatozoon. On careful physical measurement, it is found that "identical" twins do show slight differences from each other in respect of the size and relation of parts. These differences are probably due to variations in the external conditions of environment during growth. The large and obvious differences of "dissimilar" twins are, on the contrary, due to differences of the germ plasm, and are determined at the time of fertilisation of the ovum.

To mention still another theory as to the cause of variation, Montgomery considers that it is due to the disturbance of correlation of the organs, resulting from the change of environment, and is thus only indirectly due to change of environment (2).

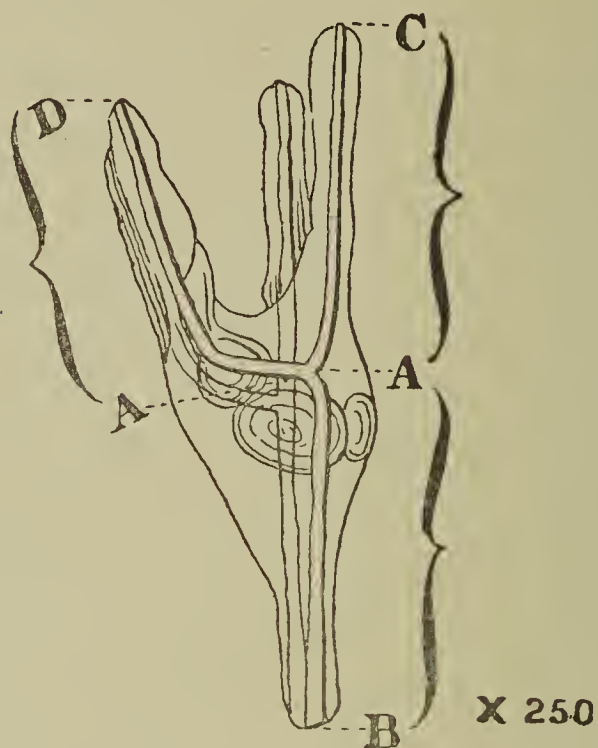
All the theories which have been advanced as to the causes of variation may thus be practically divided into two classes—(i.) theories which regard them as due to some inherent tendency of the organism to vary, or to variations of the germ plasm; that is to say, theories which are



from their nature not capable of verification by experiment; and (ii.) theories which regard them as due to the action of environment, and which are therefore to some extent capable of being put to actual experimental test.

In the present paper the writer proposes to give a short account of some experiments he has recently been making for the purpose of determining the exact amount of variation which is produced in the size of an organism by definite changes in the conditions of environment. Similar experiments have of course been made before, but as a rule the changes in the environment have been made of such a kind and such a degree as do not occur in a state of nature, and, moreover, it is but seldom that the actual numerical effect upon the size of the organism has been carefully measured. In the present experiments the changes of environment were, in the majority of cases, only such as might occur under natural conditions, and the effect produced was accurately determined by measuring large numbers of the organisms allowed to develop under the varying conditions, and calculating mean values. For such experiments as these, it is essential to work with an organism that can be readily obtained in large numbers, and which can be easily kept under artificial conditions. The larvæ or plutei of sea-urchins answer to such requirements most admirably, and they were in fact the organisms chosen. Thus these larvæ can always be obtained in innumerable quantities by the simple process of artificially fertilising ova obtained by shaking pieces of the ovaries of the sea-urchins in water, by adding other water containing spermatozoa obtained in a similar manner by shaking pieces of the testes. In a day or two these fertilised ova, which are transferred to glass jars holding 2 or  $3\frac{1}{2}$  litres of water, develop into free swimming larvæ. These continue to grow in size up to a certain point. In order to measure their size, they are killed by adding .25 per cent. of corrosive sublimate to the water, preserving them in alcohol and, after mounting them in glycerine, measuring them under the microscope with a micrometer eyepiece. These larvæ are peculiarly easy to

measure as they contain a very sharply defined calcareous skeleton, of the form shown in the figure.



In every case the length of the body AB, and the lengths of the oral and aboral arms AD and AC, were measured. In order to diminish the error of observation as much as possible, fifty larvæ were measured in each case and a mean taken; also, as a rule, several sets of observations were made in respect of each environmental condition investigated. This necessitated a very large number of measurements, so that altogether some ten thousand larvæ were measured. The larvæ were, as a rule, allowed to develop for eight days before measuring, because the arm lengths reach their maximum length in this period. After this they gradually undergo absorption.

The environmental condition investigated most thoroughly was that of temperature, because in the first place this is one which undergoes such frequent and considerable variations under natural conditions, and also some interesting and unexpected results were obtained with regard to it, which necessitated more extended inquiry. These unexpected results relate to the temperature of the water at the time of impregnation of the ova. It might be reasonably expected that the temperature would at this moment have no more influence upon the subsequent size of the larvæ than it has at any other time; but such is not the case. So sensitive are the ova and spermatozoa to tem-



perature at the time of impregnation that a difference of a few degrees of warmth or cold lasting for only a minute at this time has as great an influence as a similar difference extending over the whole eight days of subsequent development. To come to figures, it was found that as a mean of eight sets of observations, ova impregnated at about  $8^{\circ}$  C. were 4.2 per cent. smaller than those impregnated at from  $17.6^{\circ}$  to  $21.6^{\circ}$ , the subsequent conditions of development being identical. Also, as a mean of five observations, those impregnated at about  $25^{\circ}$  C. were 5.2 per cent. smaller. In all these observations the ova were kept in the cold or warmed water for an hour at the time of impregnation, but in seven other experiments they were kept for only a minute at  $8^{\circ}$  or  $25^{\circ}$ , and were then transferred to water at a normal temperature. Nevertheless the larvæ were, after eight days' growth, on an average 4.1 per cent. smaller. In four instances the ova were kept for only ten seconds during impregnation at the abnormal temperature, the larvæ being then on an average only 1.7 per cent. smaller. We may presume that the time was so short that less than half the ova were in these cases impregnated at the abnormal temperature.

In addition to the observations cited, about thirty other sets of determinations on the effect of temperature at the time of impregnation were made, some of them at temperatures, as  $15^{\circ}$  and  $23.5^{\circ}$ , intermediate between the extremes mentioned above, and others of them in which the larvæ were measured after four, five or six days' development. They all serve to confirm the fact of the special sensitiveness of the ova to temperature at the time of impregnation.

Experiments were also made on the effect of temperature during the course of development. Larvæ kept at  $23^{\circ}$  to  $24^{\circ}$  for the whole period of eight days were only about 2 per cent. smaller than those kept at  $20^{\circ}$ ; were, in fact, affected to just about the same extent as when the temperature of impregnation was  $23^{\circ}$  to  $24^{\circ}$ . Also larvæ kept at about  $15^{\circ}$  during development were about 4 per cent. smaller than others kept at  $19^{\circ}$ .

It is one of the chief recommendations for the use of sea-urchin larvæ in experiments on variation that artificial fertilisations can be carried out all the year round. In a state of nature probably these organisms only breed for a few months in the winter and early spring, but at Naples, for these experiments were carried out at the Zoological Station situated there, I was able to obtain larvæ through all the summer months. It was interesting to note, however, that larvæ obtained in these months were much smaller than those obtained in the spring, those in August being veritable dwarfs, some 20 per cent. or more smaller than those obtained in April, May and October. Those in June and July were intermediate in size. This dwarfing of the larvæ is presumably due to the comparative immaturity of the ova and spermatozoa in the off-breeding season, for the conditions of development were in other respects practically the same. It suggests a reflection as to the possibility of a somewhat similar condition existing amongst higher animals, *i.e.*, as to whether the offspring of animals conceived at the beginning or end of the term of reproductive capacity are any smaller, or less well formed than those arising in the plenitude of functional power. At present there appears to be no evidence that this is the case, though this may be due to its not having been sought for.

The next condition of environment to be examined was that of the salinity of the sea water. The larvæ were found to be exceedingly sensitive to changes in this condition. Thus larvæ allowed to develop in water to which one part in twenty of fresh water had been added, were 15·6 per cent. larger than the normal, and in that containing one part in forty of fresh water, 9·5 per cent. larger. The addition of too much fresh water has a harmful effect however, as with one part in seven of fresh water, the larvæ were 4·3 per cent. smaller. By more concentrated water than the normal the larvæ were apparently practically unaffected. This striking reaction to slight changes in the salinity of the sea water must frequently be in operation under natural conditions. Thus in the *Challenger* Expedition it was



found that, for instance, between Bermuda and New York the specific gravity of the sea water varied from 1.02504 to 1.02723 at 15.6°, or enough to cause a difference of 13 per cent. in the size of larvæ developed under the extreme conditions. The salinity of the waters of the Bay of Naples, especially near the coast, probably shows just as great if not greater variations than these.

As the salinity of the water, or percentage of inorganic salts present, has such a marked influence on the growth of the larvæ, it might be expected that they would react similarly to changes in the organic constituents present. Such proved to be the case. Thus larvæ allowed to develop in water in which other larvæ had already undergone development, and which therefore contained their products of excretion, were diminished in size some 7.5 per. cent. It was thought that this harmful effect might be partly due to the presence of uric acid and urea excreted by the larvæ, but such was evidently not the case, as the addition of small quantities of either of these salts to the water provoked a considerable increase in the size of the larvæ. Thus by the introduction of one part in 70,000 of uric acid, larvæ 12.2 per cent. larger than the normal were produced. With larger quantities of uric acid the effect produced was less, till with one part in 28,000, larvæ 2.1 per cent. smaller than the normal resulted. In water containing about one in 60,000 of urea, the larvæ were found to be about 3 per cent. larger than those grown under normal conditions. This result is very curious, and was quite unexpected. No less curious are the results of the experiments made on the effects of changes in the gases dissolved in the water. Thus it was found that the amount of oxygen gas dissolved in the water might be diminished considerably without producing any effect, and, strange to say, that the amount of carbonic acid present might be increased by some 18 per cent.; to such a degree in fact that the larvæ would barely develop at all, and yet no harmful effect on the size of the surviving larvæ show itself.

It has perhaps been noticed that no reference has been made to experiments on the effects of nutrition, this being

the environmental condition which in previous researches has generally been examined most completely, and which has been found of such powerful influence. The reason of this is twofold. In the first place, nothing is known as to the natural food of these larvæ; and in the second place, they seem to be able to develop equally well whether food is present or absent. In all probability they feed on the other minute organisms with which the sea water teems. If this is so, and if in the early stages of development supplies of food are of importance to growth, it follows that when a small number of larvæ are allowed to develop in a given volume of water they ought to grow faster than when there is a large number, for then there is only a much smaller proportionate amount of food material available. Experiment proved that within certain limits the size of the larvæ is not influenced by the number developing together. In every experiment the number of larvæ present was estimated by counting under the microscope those present in a known volume of water, and it was found, as a mean of thirty experiments in which there were on an average 4000 larvæ per litre present, the average size was almost exactly the same in thirty other experiments in which the number of larvæ was about 10,000 per litre. It was in fact found that the larvæ were undiminished in size if they were kept under about 30,000 per litre. It must be concluded therefore that in the first few days of their development these larvæ have enough food material stored in their bodies for their immediate wants.

In all the observations thus far described reference has been made only to the body lengths of the larvæ. As has been mentioned, the arm lengths were measured in addition. Hence it is possible to institute a comparison as to the effects produced in both cases. These effects, contrary to what one would suppose, run on by no means parallel lines. Thus, as we have just seen, the body lengths are practically unaffected by the number of larvæ developing in a given volume of water. The arm lengths react most markedly, so that with 4000 larvæ per litre the aboral and oral arm lengths are respectively 13·4 and 15·9 per cent. shorter than



with 500 per litre; and with 17,500 per litre they are respectively 25·9 and 23·3 per cent. shorter. Variations in the temperature of the water during development also produce opposite effects in the two cases. As we have already seen, the body lengths of larvæ allowed to develop at temperatures above 22° are about 2 per cent. shorter than of those at about 20°, but the aboral and oral arms are respectively 10·8 per cent. and 8·5 per cent. *longer*. Again, whilst the body length of larvæ grown in diluted water is on an average increased by 9·1 per cent., the arm lengths are *decreased* by 7·7 and 10·5 per cent.; or, as the arm length values are calculated as percentages on the body lengths, they are practically not affected at all. Even the arm lengths are not affected to the same extent by the same change of environmental condition. Thus the ratio between the arm lengths of larvæ grown at temperatures above 22° is 4·3 per cent. higher than of those at temperatures below 18°.

It is unnecessary to make remark upon the experiments made in respect of other conditions of environment, but a passing notice may be given to the observations which showed that the variability or amount of variation in the size of the larvæ may be affected by changes in the environment, as well as their actual average size. Thus the dwarfed larvæ obtained in the summer months varied in size some 10 per cent. more than those obtained in the spring. Again, larvæ allowed to develop at 19° varied 18 per cent. more than those allowed to develop at 17°, and 10 per cent. more than those at 23°. It would seem therefore that the variation in an organism, whether it be in degree or in the average size, with reference to a single organ or to the correlation of organs, is equally capable of being affected by changes in the conditions of environment.

This conclusion is fully supported by the results of the measurements made by Weldon upon shrimps and crabs (5). By measuring some hundreds of individuals, and taking mean values, Weldon showed that the specimens obtained from various sources did not by any means correspond in respect of the size and relation of their parts, but that they

may be looked upon as so many local races. Thus, for instance, whilst shrimps obtained near Plymouth had a mean carapace length of 250·05, those from Southport had one of 248·50, and those from Sheerness one of 247·51. The degree of variability also differed in each case, the "probable errors" being respectively 4·53, 3·17 and 3·05. Also, different organs varied to different extents. For instance, the post-spinous portion of carapace reached the maximum length in Sheerness shrimps and the minimum in those from Plymouth, whilst as we have just seen the carapace lengths varied in the opposite direction. Still again, the correlation between the various organs also varied in the different local races, though this variation was small and might perhaps have been due to experimental error.

A few remarks may be made as to the bearing of the results obtained in these experiments on the theory of Natural Selection. It has been shown that a change in the salinity of the water in which the larvæ are developing may produce a variation of 15 per cent. in their size. Now these individual larvæ are found to vary on an average by about 6 per cent. from the mean size of the whole number. If, therefore, half of a number of larvæ developing in any region were exposed to water of one degree of salinity and the other half to water of the other degree, the variability of the whole group of larvæ would be more than trebled. Other changes in the environment would produce similar, though perhaps smaller, changes. Now, other conditions equal, the more variable an organism, the greater opportunity has Natural Selection of stepping in and, by preserving the most favourable individuals, modifying the species. But, it may be objected, this is not actually the case, because the variations thus produced are, in Weismann's terminology, merely somatogenic and not blastogenic. They are merely variations in the body tissues, and, the germ plasm not being affected, are not transmissible by heredity. A little reflection will show that this objection, though in some respects valid, yet is by no means fatal to our proposition. Thus, suppose that for instance in sea-



urchin larvæ there was a tendency for the larger individuals to be preserved by the action of Natural Selection. When the individuals vary on an average by only 6 per cent. they are all so similar in size that the advantage the larger individuals have over the smaller in the struggle for existence is only very slight, and hence Natural Selection can only act very slowly and haltingly. Suppose, on the other hand, that by the action of varying conditions of environment the larvæ vary on an average by 20 per cent., then the larger individuals will have a very much greater advantage over the smaller ones than before, and will consequently be preserved in much greater proportionate numbers. Now these larvæ, though caused by the action of a variable environment to assume a considerably larger size than they would have had under a more constant one, would nevertheless under this more constant condition have still been of larger size than the other individuals, and hence will transmit to the next generation that characteristic of increased size, though to a smaller degree. Thus though the selected larvæ might be 20 per cent. larger than the average, they only contain a similar germ-plasm to larvæ 6 per cent. larger than the average when grown under a more constant environment. Hence their offspring will only be some 6 per cent. larger than those of the previous generation.

We now see the importance of the fact established in the earlier part of this paper, *viz.*, that the ova are more sensitive to changes of environment, such as temperature, at the time of impregnation than subsequently. Thus, whilst the temperature of the water in which these larvæ develop under natural conditions may show but slight variations on an average in periods extending over several weeks, yet the extreme variations within such a period may be considerable. As, therefore, ova would probably happen to undergo impregnation at all times in the breeding season, whatever the temperature of the water, the larvæ developed therefrom would have a greater variability than if the ova had been no more sensitive to temperature at one time than at another. Though it has not been conclusively proved that the ovum is specially sensitive at the time of impregnation

to other conditions than that of temperature, yet the probability is that such is the case, and that conditions such as the salinity of the water also have a more powerful influence.

Another conclusion arrived at, which is of some importance in the study of the problems of variation, is that changes of environment may produce different and opposite effects upon different parts of the same organism. Thus a fall in the temperature or a decrease in the salinity of the water produces a decrease in the arm lengths of the larvæ and an increase in the body length. It is thus possible for parts of an organism to become modified, though they may be entirely unacted upon by the process of Natural Selection, or may even serve some useful purpose to the animal. If, for instance, it is of greater utility to the larvæ that their body lengths should increase than that their arm lengths should increase, and if by the action of a fall in the temperature of the water larvæ with greater body lengths and smaller arm lengths are produced, then, on an average, the larvæ exhibiting these changed characteristics to the most marked extent will survive, and the race will be modified in this direction.

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## ON THE PHYSIOLOGY OF REPRODUCTION IN PLANTS.<sup>1</sup>

BEHIND every morphological phenomenon there stands a physiological question. Problems which can be tentatively dealt with in two ways, according to the relative importance assigned to the morphology and the physiology of the organism are still continually arising in Botany, as they have arisen—in various guises—in the past, and it would probably be not difficult to classify most of the combatants in the great disputes of the science into two groups, the one including those who are especially prone to judge biological causes on physiological evidence, the other those who regard morphological data as of primary importance.

The point of view has exerted considerable influence in the study of plants, whether we turn our attention to textbooks or to the monographs of the investigator, and the warnings prompted by the clear-sighted vision of a few strong observers, of the dangers of allowing Botany—the study of plants—to be torn into shreds of narrow specialisation, superficial generalisations, and mere vapourings of transcendentalism, are justified by the departures of the last twenty years.

<sup>1</sup> Die Bedingungen d. Fortpflanzung bei einigen Algen u. Pilzen. Von Professor Dr. G. Klebs. Jena, Gustav Fischer, 1896.

Beiträge zur Lehre von der Fortpflanzung der Gewächse, von Professor Dr. M. Möbius. Jena, Gustav Fischer, 1897.

In no branch of the subject have these dangers been more apparent than in the study of the Thallophytes ; though, possibly, examples are oftener quoted from among the Flowering Plants, because the facts seem easier to obtain and more obvious.

The morphological doctrine known as the alternation of generations is a case in point with reference to the former ; while the disputes as to the relation of highly adapted—specialised—plants, such as *Xerophytes*, to their environment afford examples in the latter connection.

It being admitted that the alternation of generations as matter of fact exists in the *Bryophyta* and *Pteridophyta*, the attempt to read the dogma into the life history of the Thallophytes has been made so often and so persistently that the unwary or insufficiently informed are liable to suppose it is more successful than is really the case, while even more cautious speculators seem to be persuaded it is necessary—a consequence of persistence as it were.

Again it occurs, largely owing to misapprehensions of the real difficulties which Darwin saw so clearly, that some botanists regard the case for a Xerophyte—as a particular example—being structurally the direct outcome of the persistent actions of the environment, as much more nearly capable of demonstration than the present condition of science allows.

Morphologists divide the life-cycle of a Moss into two parts. The Moss-plant (*Gametophyte*), arising as a vegetative outgrowth from the protonema of the germinating spore, ending in the production of the oosphere, etc., being the one ; the Sporogonium (*Sporophyte*) constituting the other.

If we ask why *two* generations? Why the profound structural differences between the protonema and the leafy stem, their sharp segmentation, entire change of growth, cell-division, etc., do not justify our making a third break here in the life-cycle? The morphologist replies because the organic separation between embryo and gametophyte on the one hand, and between protonema and sporophyte on the other, are so complete that in each case a breach of



organic continuity is established which justifies our regarding the two alternate "generations" as we do. It is clear, however, that some assumptions lie behind this, and that tacit necessity for fitting in the life-history to the ascertained alternation in Ferns plays some part; for, in the first place, mere breach of continuity would apply to any naturally separated tubercule or bud or even a piece of protonema, and, in the second, we know that the protonema need not arise from a spore, but may be developed from any part of the gametophyte or sporophyte—*e.g.*, a rhizoid, a piece of stem, or of seta, etc.

Obviously one underlying assumption is that the normal life-history does not admit of the breaches of vegetative continuity, or of the "misplaced" origins of protonema referred to above.

But *normal* means *usual* in these cases. The same applies to the Ferns, where apospory and apogamy have now, moreover, been shown to be so common that one is almost driven to ask how soon it will be necessary to take a sort of census as to the proportion of cases where "normal" alternations of generations occur, and those where we find the new Fern-plant—the *Sporophyte*—springing direct from the previous sporophyte without the intervention of the gametophyte-generation; or sporangia springing direct from the prothallus, and so on.

The absolute number of these "abnormal" cases is at any rate large, and when we come to look over the whole domain of the Cryptogams, our doubts as to any fixed *necessity* for the alternation of generations increase in proportion as the question, How far is it all a matter of conditions of nutrition, moisture, illumination, temperature, etc.? assumes definite shape. For however much we may assent to the typical character of alternations of generation in *Bryophyta* and *Pteridophyta*, we must concede that such alternation is not essential, and the gradual reduction of one generation in the higher plants till it is merely represented by the most obscure traces, detected only with difficulty and by special methods, is a further proof of this.

Returning to the second of the classes of cases selected above—How far may we conclude that the peculiar organisation of such specialised plants as Xerophytes, for instance, are due to the continued action of their present environment, and how far to the accumulated inherited effects of the environment in the past? For that is what the dispute between the two great schools amounts to. In other words, how far will the plant continue to build up its structures and assert its morphological individuality, independently of variations in the environment, in virtue of the machinery it possesses being compelled to work along definite lines if the environment allow it to work at all; or how far can the action of the existing environment affect the working of that machinery in the present, and bring about variations which we can detect?

It is clear that experiment alone can give us information here; but the results of the experiments already made go to show that we have still much to learn before we can even realise the nature in detail of the problem to be attacked.

Are we, when experimenting with a varied environment, directing its actions on to a complex of structures which are themselves the response to the continued action of this environment; or are other factors in play—*e.g.* the accumulated and emphasised results of previous environments handed down by heredity?

Most botanists would probably say the latter, and indeed it seems difficult to see how the former could be maintained, although some such assumption would appear to lie at the foundation of some of the experimental enquiries started or proposed.

It seems evident that a clear apprehension of this question must precede any enquiry into the action of the environment on plants, but that once obtained we need not be deterred even by the enormous complexity of the subject from admitting that all the phenomena of morphology, including the alternation of generations, are phenomena with physiological questions behind them, and therefore subjects for experimental enquiry.

Glimpses are already to hand which show that such is



the case. Some Liliaceous plants never produce seeds, unless experimentally forced to do so, because the stores of food-materials are all deflected into the bulbs—the rudimentary gametophyte is starved and dies of inanition, and yet we have no reason to believe that the ever-continued sporophyte suffers. Species of *Musa* and many other plants have probably never formed seeds for thousands of years, and in such cases as these and the potato and many other flowering plants, where the sporophyte is propagated vegetatively, we have no reason to believe that the plant suffers, though in many of them no trace of the gametophyte generation ever appears at all.

It looks then as if the environment may have more to do directly with the origin of reproductive organs—and with that of other structures also, be it said—than is often assumed.

In these classes of cases it is soon evident that matters are too complex for direct experimental treatment, at least just now, and we may feel very sure that all hope of solving fundamental questions concerning the relations between the morphology and physiology of sexual organs must be approached through the lower and simpler forms of life. Striking illustrations of variation, or of morphological inconsistency, are doubtless more easily obtained from higher plants than from lower, and probably because the very complexity of their organisation renders them more easily varied—deflected out of the normal course—on a similar principle to that which renders a tall house of cards more easily overthrown by a shock than a less ambitious erection would be; but when it comes to studying the factors at work which induce the variations it is perhaps logical to expect that the study of the lower plants will be more productive of results. But we must not forget that a very slight variation in a lower plant may imply more than a much more obvious change in a higher one.

In this connection the recent publication of Kleb's experiments on the conditions affecting the development of reproductive organs in some Algæ and Fungi is one of the most valuable and stirring contributions to botany of this decade.

Klebs' book *Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen* will have a peculiar value to all botanists interested in Cryptogams and especially in Thalophytes, and this in three connections. First, it is a record of very numerous and careful observations of the conditions affecting the life of several types of fresh-water Algæ, and of experiments pushed so far that it seems now possible to be sure of growing these particular forms at will in the laboratory by insisting on the maintenance of the conditions. That this will be a boon to those who have hitherto depended on accidental supplies of Algæ from outside, hurriedly collected and brought the day before into an environment which may be detrimental or not to these delicate organisms, is obvious; but it will also afford much help to those who have had sufficient experience to know what Algæ they can and what they cannot grow in the laboratory, and must lead to extensions of power in this connection.

Secondly, Klebs gives very clear directions for the separation and pure culture of minute and intermixed fresh-water Algæ on solid media and in liquids, and it should be a stimulus to many new departures when it is known that these organisms can be treated in similar ways to Fungi and Bacteria in this respect. True, we have known for some time that something may be done towards isolating pure cultures of Algæ, and Beyerinck and others have given clear indications of success, but Klebs carries this subject further than ever before, and shows how we may look for rules of isolation and pure cultures of Algæ as trustworthy as those for other organisms. The application of all this is obvious, but Klebs points the moral by himself showing that even observers so astute and able as Woronin and Rostafinski confounded two organisms in their celebrated study of *Botrydium*, and puts this so convincingly that Strasburger has accepted and already reproduced the result in his recent edition of the *Botanische Practicum*, just published. The criticism of those startling observations which Chodat,<sup>1</sup> Borzi and others have recently

<sup>1</sup> Chodat has replied to Klebs in a recent number of the *Arch. des Sc. Phys. et Nat de Geneve*, t. iii., Jany. 1897.



offered on the polymorphism of the lower green Algæ, stands so firmly on the new foundations which Klebs gives it, that one is constrained to believe much of this work must be re-examined by the help of the strict methods enjoined by him.

Thirdly, the especial object of the work is to show that, having learnt to isolate and grow a green Alga, its behaviour will vary according to the conditions of the environment. This of course would be generally conceded, but the point is that the exact conditions which induce or govern a given biological reaction can be discovered and controlled, and so our knowledge is altered from an indefinite conviction that you must not do this, that, or the other, to an Alga, or it will not grow, or multiply, or succeed generally, to the definite surety that if you want a given Alga to produce zoospores you must treat it in such and such a manner, and if you alter the treatment according to directions you can make the Alga form sexual organs, and so on.

It sounds almost absurdly impossible when put in such a form, and yet many of Klebs' experiments show that his fifteen years or so of study of these reactions have resulted in knowledge so clear and so definite of the exact conditions necessary to induce a given biological response, that one may almost compare the operations with those of a chemist who calls forth a predicted change in a substance in a test tube by adding another substance to it.

When we are told that *Conferva*, for instance, after being cultivated for twenty-two days in a 1 per cent. galactose solution, in which it forms no zoospores, at once proceeds to form them if transferred to a solution of aesculin, and that the whole experiment is carried on in the dark, our ideas begin to receive shocks which lead us on from total revolt to wondering acquiescence and conviction in proportion to our acquaintance with the number of recorded experiments, the care and fulness of the records, and the character of the evidence generally.

But the work teems with equally startling results, of which I shall have space to quote a few instances only.

*Vancheria repens*, if growing on solid media in damp

air in the light, can be kept for months and years without forming zoospores; yet at any time zoospores can be obtained by plunging it into water.

The alga can be cultivated easily in the well-known Knops' nutritive fluid of inorganic salts, and in 0·2-0·5 per cent. solutions grows well but forms no zoospores so long as the salts are supplied; yet at any time vigorous plants removed to pure water at once develop zoospores.

Cultures in water only, or in very dilute salt solutions—0·1-0·2 per cent.—in the light, remain sterile: but darkening them more or less completely at once induces zoospore formation.

If exclusion of light is combined with either of the two foregoing methods the stimulus to zoospore-formation is quickened.<sup>1</sup>

In these cases the first zoospores appear in less than twenty-four hours, and go on forming for weeks. A most interesting discussion follows as to the nature of the changes.

This is supplemented by experiments on the effects of temperature, various light-rays, osmosis, organic nutritive materials, mechanical stimuli, etc, and even if the reader does not accept all Klebs' few and cautious conclusions as to the probable actions of the various factors, he can scarcely escape two convictions, *viz.*: (1) that in such an Alga, every factor of the environment produces its own effect as it varies, and (2) Klebs has shown that strict experimental methods can be applied to the solution of the problem as to what that effect results from.

It is premature to generalise widely from the results of this work, since Klebs promises us another book containing his conclusions, this first instalment being confined almost entirely to the detailed descriptions of the experiments. Nevertheless one cannot avoid drawing comparisons between the effects of light, temperature, moisture, food-materials, etc., in stimulating the production of asexual or sexual organs in these Thallophytes, and the effects of the same agents in forcing higher plants to propagate by

<sup>1</sup> The general truth of this has been confirmed by Miss Pertz in the laboratory in Cambridge.



asexual organs or to flower. The results are not always the same, however, in either case. At the outset, some species respond to a given stimulus fairly readily: others again show little or no response, and it seems as if much yet remains to be done ere we can explain the specific differences.

One is struck with the apparent similarity between the cases where *Vaucheria* remains sterile in moving water, as Klebs finds, and those of many flowering aquatics which are also sterile in quick streams. Schenck,<sup>1</sup> for example, says species of *Hippuris*, *Sagittaria*, *Alisma*, *Juncus*, *Littorella*, *Elatine*, *Sparganium*, *Callitriche*, *Potamogeton*, etc., remain sterile in moving water; and Klebs found that, like *Vaucheria*, *Ulothrix* and *Ædogonium* are both induced to develop zoospores by removal from moving water—which inhibits the process—to still water. Even slowly running water inhibits the formation of sexual organs in *Ædogonium*, and Klebs quotes an experiment (p. 279) where a culture which remained sterile from the 10th of June to the 20th of July in the moving water of his aquarium, at once developed the sexual organs when removed to quiet water. As to *Vaucheria*, he declares that species which remain sterile for months in running water at once form the sexual organs if transferred to still water. The discussion as to possible factors of explanation is very interesting, but too long to reproduce; he cannot explain it in detail. Another interesting point is the experimental proof that transpiration into a relatively dry atmosphere is an essential condition for the development of the conidia of *Eurotium*; and we have convinced ourselves in the Cambridge Laboratory that sexual organs or conidia can be produced by following the directions; and here again one is tempted to draw comparisons with the numerous cases where the on-coming of a dry atmosphere favours the flowering of higher plants, as pointed out by many observers. Möbius,<sup>2</sup> among others has collected cases showing that dry air and a moist soil

<sup>1</sup> *Biologie der Wassergewächse*, p. 107, 1866. Cited by Möbius, p. 130, *Beiträge zur Lehre von der Fortpflanzung*.

<sup>2</sup> Beilage zur Lehre von der Fortpflanzung.

will often bring plants to flower which refuse to flower otherwise, or only to a less extent.

Over and over again attempts have been made to correlate the conditions of the environment and the habit of the plants subject to it, some of the most recent being Warming (*Ökologische Pflanzengeographie*, 1896), Gaston Bonnier (*Influence de la Lumière électrique sur la forme, etc.*, *Rev. Gen. de Bot.*, 1895) and Moebius (*Beiträge zur Lehre von der Fortpflanzung*, 1897), but the critical reader always feels that even the most careful experimenter is unable to solve such problems, for two chief reasons: (1) The (higher) plants experimented upon are so exceedingly complex that it is almost impossible to disentangle the reactions to the conditions imposed by the experimenter, from correlated internal changes, and (2) it seems as yet impossible to vary one factor of the environment without at the same time causing others to vary also. For instance, in experiments with higher plants, we cannot modify the intensity or quality of the *light* by means of screens, etc., without at the same time altering the *temperature* of the soil, plant or air: if we vary the *temperature*, then changes in *moisture* are induced, and so on.

Now Klebs has chosen subjects and methods which reduce these difficulties to a minimum. By selecting Algæ, which grow at low temperatures and in water, and by confining his attention to the conditions which affect reproduction, he is able to go nearer to the ideal variation of one factor at a time than most experimenters have done.

The principal Algæ employed are—*Vaucheria*, *Hydrodictyon*, *Botrydium* and *Protosiphon*, *Spirogyra*, *Desmids*, *Ædogonium*, *Ulothrix*, *Hormidium*, *Conferva*, *Bumilleria*, *Stigeoclonium*, *Draparnaldia*, *Chlamydomonas*, and *Hydrurus*.

A brief outline of his programme with *Vaucheria* will serve as an index to his choice of conditions. He first investigates the effects of nutrition, moisture, light, temperature, inorganic salts, organic compounds, osmosis, acids and alkalies, the partial pressure of oxygen and the effects of moving water, on the development of the asexual



zoospores ; and then he tries their effects on the development of the sexual organs.

Some results have been referred to. The difficulties with light are great, but he comes to the conclusion that apart from the assimilation effects, light-rays have an influence of their own in inhibiting the development of zoospores. Within the wide range of temperature ( $3^{\circ}$ - $26^{\circ}\text{C}$ ) at which *Vaucheria* will grow, the lower temperatures ( $3^{\circ}$ - $8^{\circ}\text{C}$ ) stimulate, while higher ones inhibit zoospore-formation.

Some curious results are obtained with inorganic salts. Plants growing actively in nutritive solutions of suitable strength refuse to form zoospores, and even darkening them—usually a most effective method—will not stimulate to zoospore-formation until the solution is diluted below a certain point. Removal to pure water, however, at once causes them to develop zoospores, and especially if darkened at the same time. It is curious that these effects can be got with solutions of sodium chloride and other salts not usually regarded as nutritive.

Yet this effect cannot be got by transference from sugar solutions to water : though it can if the Algæ be transferred from air or water to the sugar solution.

Camphor gave extraordinary results. After eleven days in camphor-water, transference to water caused zoospores to form : on adding camphor again, the process was inhibited, and even darkening failed to bring them—yet after four days in this inhibited state, removal to water induced the formation of zoospores in twenty-four hours, and the Alga went on developing them for a week or two : a re-addition of camphor at once stopped it, but removal to water at once stimulated again, and so on.

An interesting discussion follows as to whether the above were osmotic effects, and comparisons of the osmotic equivalents convinced Klebs that the explanation is not to be found here. Nor does the (slight) acidity or alkalinity of the medium explain it, as experiments show.

Oxygen is not necessary, and some surprising results are obtained as to the small quantities of oxygen needed

even for growth ; darkened cultures go on producing zoospores for weeks.

I have already referred to the startling results obtained with running and still water.

As regards the sexual organs, affairs are very different. In the first place bright light is necessary for their formation, and secondly, sugar increases the tendency to form them. Cases are quoted where *Vaucheria* was kept growing for four and a half years in salt-solutions absolutely sterile : yet, at any time, removal of a portion to sugar-solutions, and exposure to bright light, induced the formation of sexual organs in four to five days !

It is not a simple question of nutrition, though the sugar is evidently used to afford nutriment ; for if fed with sugar in the dark no sexual organs are developed, while they form in the light whether carbon dioxide be excluded or not.

Further experiments convince Klebs there is a light-effect over and above that of assimilation ; but that only the inception of the sexual organs depends on light-action, for once incepted they can be made to complete their development in the dark—no new ones forming meanwhile.

The conditions being known, it is easy at any time to obtain pure growths of sterile *Vaucheria*, and with such Klebs found by means of artificial lights the intensity and quality necessary to induce the formation of sexual organs. The experiments with coloured screens are not devoid of ambiguity, but the rays at the violet end of the spectrum seem necessary.

It is impossible to give even a sketch of all the experimental results, and I must conclude with a reference to the marvellous control obtained over the development of the male organs. *Vaucheria repens* normally produces one oogonium and one antheridium side by side at intervals along the filament : by raising the temperature, or by diminishing the air-pressure, Klebs was able to force all the young oogonia to grow out to vegetative branches, or to suppress them altogether, and to increase the antheridia up



to as many as three to seven in a group—in short to convert the hermaphrodite plant into a male one, at the expense of the female organs. It would be interesting to learn how far the spermatozoids are capable of function. The converse conversion could not be made.

No less interesting are the results with other forms. Parthenogenetic spores were produced in *Spirogyra* by plunging the conjugating threads into selected salt-solutions at the critical moment when union of the zygotes was first about to be accomplished; both “male” and “female” cells were thus converted in spores capable of germination. Similar artificial productions of parthenospores in *Ulothrix*, *Chlamydomonas*, etc., were also accomplished.

The inhibition of the zoospores in *Ædogonium* by light or by running water—this plant was so wonderfully under control that the author could make it develop zoospores or sexual organs at will by altering the conditions in definite ways—the artificial regulation of the sexes in *Ulothrix*, etc., as well as many other points must be passed over here.

*Hydrodictyon* affords one of the best examples of all for showing how conditions rule the development of reproductive organs. It practically amounts to this. In any cell of the net, it is possible at any time to cause either asexual zoospores or sexual gametes to be developed by varying the conditions in definite ways. There are perhaps limits to the size of the cells—they must not be smaller than about 0.03 mm. for gametes and 0.2 mm. for zoospores—but at any time during their growth to a length of 10 mm., external conditions will determine whether growth shall continue, or the contents be converted into zoospores or into gametes. Klebs expressly states that he knows no other Alga which is so plastic in these respects, for every vegetative cell is equally capable of forming, at any time, either zoospores or gametes according to the conditions imposed. The importance of these facts with respect to any hypothesis of alternation of generations is obvious.

Enough has been given to show that Klebs' book will have to be reckoned with as one of the best attempts yet

made to bring into the sphere of actual experimental enquiry a subject which has baffled physiologists for a long time.

If we attempt to see what light this throws on the question of alternation of generations the following remarks occur to one :—

Among the Thallophytes we meet with sporogenous tissues giving rise to asexual spores, and with oospores developed sexually, but if we attempt to read into these and their sequence the dogma of alternation of generations, some quaint difficulties arise.

One of the most convincing cases to many minds is that of such Algæ as *Ædogonium*, *Coleochæte*, etc., where if we call the plant or portion which bears the sexual-organs a gametophyte generation, we have to face the difficulty that it may at the same time bear asexual spores. The attempt to get over this by terming asexual spores borne by the gametophyte *gonidia*, and reserving the term *spore* for bodies *indistinguishable from these gonidia by any morphological or physiological character whatsoever* beyond their origin from a so-called sporophyte,<sup>1</sup> carries its own refutation.

Now the principal interest of Klebs' work centres in his proof that asexual zoospores as well as sexual organs can be called forth or suppressed altogether, practically at will, in any part of the life-cycle of even so highly developed an Alga as *Ædogonium*, or of so specialised a Fungus as *Eurotium*, by merely altering the conditions of the environment. To speak of alternate generations in such cases seems impossible: the assumed mark of a generation is here a matter of conditions, simply, and cannot be regarded as a morphological necessity coming into evidence at just such a place and such a time in the life of the plant as is demanded by some special structure and working of the organisation from the beginning.

Few Algæ have been more thoroughly studied than *Ulothrix zonata*; but Klebs shows that it depends on conditions whether a filament forms (1) Zoospores with four

<sup>1</sup> A point already insisted upon by Scott also in his address to Section K, British Association, Liverpool 1896, p. 7.



cilia which at once germinate directly, (2) smaller Micro-zoospores with four or two cilia which also germinates directly, (3) still smaller Gametes with two cilia, which either conjugate and form zygospores, or can be made to act as parthenospores without conjugating, and (4) larger fusiform Zygospores with four cilia. Moreover, in the origin of the zoospores, etc., from a cell, it is a matter of conditions (chiefly nutrition and size) whether one, two, four, eight, or even sixteen or thirty-two zoospores are formed in a cell; or whether eight, sixteen or thirty-two micro-zoospores or gametes are formed in one cell, and so on.

One is also struck with the fact that although Klebs resorts to extreme measures in some of his experiments, in the majority of cases the changes of environment are just such as may and do occur in nature.

The following remarks (p. 175) seem worth careful note :—

“Es ist merkwürdig, dass aus der Geschichte der Wissenschaft so wenig gelernt wird. Schon zweimal hat in der Botanik der gleiche Streit über den Polymorphismus geherrscht, zuerst bei den Pilzen und dann bei den Bakterien. Beide male ist dieser Streit aus unfruchtbaren Diskussionen in die richtigen, streng wissenschaftlichen Bahnen geleitet worden, als man die Reinkultur der Organismen als notwendigen Ausgangspunkt für jede Untersuchung in dieser Richtung verlangte.”

While Klebs' book is a model of records of experimental work, full of new points and suggestions, Möbius' “Beiträge zur Lehre von der Fortpflanzung der Gewächse” is rather an interesting *resumé* of facts compiled from various authors who have written on the reproduction of plants. It consists of five chapters; the first an introductory one dealing with the meaning of individual reproduction as related to the maintenance of the species, and the significance of vegetative propagation as opposed to sexual reproduction proper. The point of view is elementary, but a number of interesting facts are collected, and I think he is quite right in insisting on the plant as an individual

and refusing to treat seriously the proposition that all the poplars in France are only parts of an individual. Chapter II. is concerned chiefly with a discussion of the question whether continued vegetative propagation is injurious to the constitution of plants like the Banana, Potato, Poplars, Fruit-trees, and numerous other plants—wild as well as cultivated—which are rarely or never grown from seed. His views are similar to those of a recent American author who has written clearly and suggestively on this subject,<sup>1</sup> and may be shortly put as summing up against the view that varieties or species show signs of deterioration or dying out from this cause.

In the third chapter Möbius discusses the conditions on which the flowering of plants depends. The influence of light, temperature, moisture, and nutrition, etc., are successively examined, but although the facts collected are interesting one feels dissatisfied with the results, partly owing to the cause already mentioned—that experiments in this domain involve such complexities that one is never sure that the response is to a given factor of the environment—and partly because the whole work seems hurriedly written.<sup>2</sup> Moreover, in this chapter the author gives the only experiments quoted which he has himself performed, and they are distinctly unsatisfactory.

In chapter four, the relations between bud-propagation and reproduction by seeds is discussed, with much reference to Darwin's celebrated chapter in his "Variation of Animals and Plants under Domestication".

By far the most interesting part of the book to most botanists will be the last chapter, in which the author gives a summary of the origin and significance of sexual repro-

<sup>1</sup> T. H. Bailey, *The Survival of the Unlike*, 1896.

<sup>2</sup> This latter conclusion is borne out by the misprints which are too common (and evidently not all printer's errors) here and elsewhere in the book, *e.g.*, "Do the Musa show any signs of deterioration" (a quotation on p. 34), *Bülhen* for *Blühen* (p. 84), *Laryx* for *Larix* (p. 88). Two errors in a quotation on p. 110. *Ranuncutus* (p. 138). *Musa sapientium* instead of *sapientum* repeatedly, and also *Himanthallia* for *Himanthalia* several times.



duction in plants. What is meant by "Die ungeschlechtliche Bildung von Keimen unterbleibt bei den Blütenpflanzen" (p. 162), I do not quite see, unless the author denies that pollen grains are spores, etc. Möbius regards sexual reproduction as advantageous in three ways, (1) Legitimate crossing of individuals helps to fix the characters of the species, (2) Crosses of more remote individuals offer increased opportunities for variations on which natural selection can work, and (3) sexuality gives a means for developing more complex and highly differentiated forms.

H. MARSHALL WARD.

# CONDENSATION AND CRITICAL PHENOMENA.

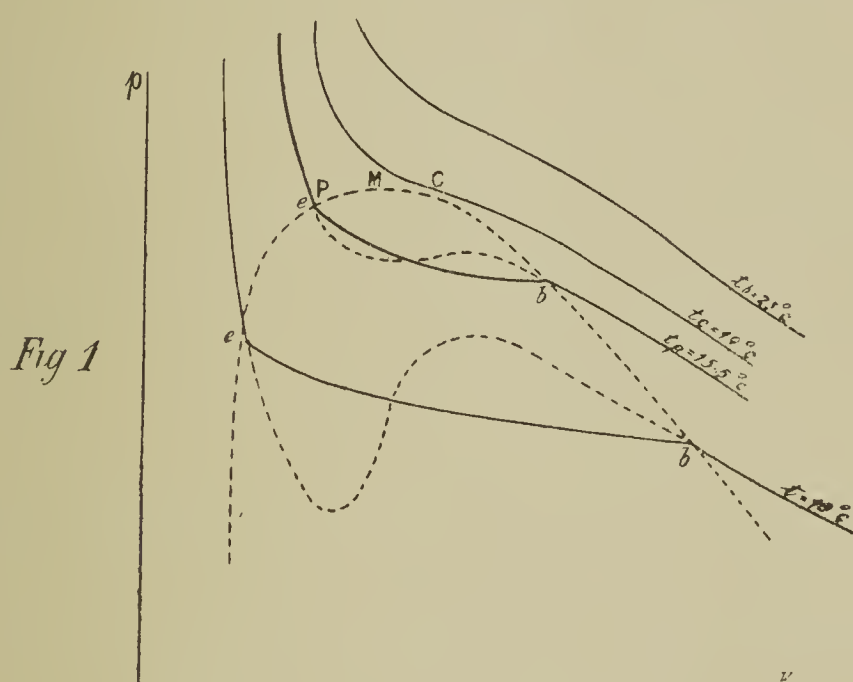
## II. MIXTURES OF TWO SUBSTANCES.

THE phenomena which are displayed by mixtures during condensation and near the critical point are more complicated than those of single substances, so much so that a complete explanation of the behaviour of mixtures was not obtained till the phenomena were unravelled by the application of thermodynamics.

Suppose a certain volume of carbonic acid is mixed with a fifth of its volume of air at  $0^{\circ}\text{C}$ . and one atmosphere. Let us define the composition of a mixture as the volume of one of the constituents, here say carbonic acid, in unit volume of the mixture. The composition  $x$  of this particular mixture would then be  $5/6$ . Its properties were investigated by Cailletet and afterwards by the writer of this article. At the temperatures of the experiments, air behaves like a single gas, and the mixture accordingly like a mixture of two substances. When this mixture is compressed at  $10^{\circ}\text{C}$ . the volume diminishes regularly until at a certain moment some liquid is formed. This liquid consists of liquid carbonic acid with some air dissolved in it. As compression goes on the quantity of the liquid increases, but the pressure instead of remaining constant during the process of condensation, as with single substances, goes on rising all the time until the whole of the mixture is in the liquid state. As was shown in the first part of this article even a small quantity of a foreign body is sufficient to bring about an increase of the condensation pressure at diminishing volume. For an actual mixture like the one which we are considering this rise of pressure is much more marked, and amounts to several atmospheres. If we look upon the pressure in the usual way as consisting of the sum of the partial pressures for the two constituents we can easily understand why the pressure should be higher the smaller the volume. The partial pressure for carbonic acid is equal to the vapour



pressure at  $10^{\circ}\text{C}.$  and therefore constant, but the pressure of the air becomes higher and higher, and the total pressure must therefore also rise with compression. Taken in this way the problem would be one of the absorption of a gas by a liquid, and of the validity of the laws of Dalton and Henry. But these laws, though capable of describing the phenomena in a few cases and under special conditions which need not be stated here, are as a rule inadequate, and more especially so the nearer one gets to the critical point. The problem must therefore be taken up in a different manner and the first step is to draw diagrams for mixtures in the same way as this was first done by Andrews for single substances. The changes of pressure and volume for our mixture at  $10^{\circ}\text{C}.$  are given diagrammatically in fig. 1 by the isothermal  $t=10^{\circ}\text{C}.$  At  $b$  the conden-



sation begins, at  $e$  it is finished. The curve shows the rise of pressure in the gaseous state, a break at  $b$ , the rise of pressure between  $b$  and  $e$ , another break at  $e$  and a very steep curve beyond  $e$  in the liquid state. Curve  $t=25^{\circ}\text{C}.$  shows the behaviour of the mixture at  $25^{\circ}\text{C}.$  This curve has no breaks. The mixture does not show any condensation and must evidently be above its critical temperature. Experiments have shown that the mixture cannot be condensed at temperatures higher than about  $19^{\circ}\text{C}.$  This temperature may therefore be called the critical temperature of the mixture, and it appears that the addition of one fifth of air has lowered the critical temperature considerably. In

compressing the mixture at a temperature below  $19^{\circ}\text{C}.$ , say at  $18^{\circ}\text{C}.$ , an entirely new phenomenon is observed. The liquid appears as at  $10^{\circ}\text{C}.$  at a certain volume (point *b* of the isothermal) and the pressure goes on rising after that; the liquid increases at first but its surface becomes less and less sharply defined and long before the whole of the mixture is liquefied the surface becomes a mist and disappears altogether in very much the same manner as the liquid surface of a single substance disappears at its critical point. On lowering the pressure the mist and the liquid surface reappear at about the same level where the disappearance took place before, and further lowering of the pressure gives the phenomena of compression in the opposite order. Similar phenomena are observed at lower temperatures, but the lower the temperature the larger the quantity of the liquid phase is when the surface disappears or reappears. Below  $15^{\circ}\text{C}.$  the whole of the mixture is liquefied, as described for the temperature of  $10^{\circ}\text{C}.$  If we call the disappearance or reappearance of the liquid surface in a mist the "critical phenomenon" we may express the experimental results by saying that the mixture shows the critical phenomenon not at one temperature only, but over a range of temperatures of about  $4^{\circ}\text{C}.$  ( $15^{\circ}\text{C}.$ - $19^{\circ}\text{C}.$ ). By saying that  $19^{\circ}\text{C}.$  is the critical temperature for our mixture we evidently do not exhaust the phenomena. Above  $19^{\circ}\text{C}.$  no condensation takes place, but the critical phenomenon is not confined to that temperature but occurs at lower temperatures also. In fact as will appear presently the critical phenomenon really belongs to a temperature lower than  $19^{\circ}\text{C}.$  (about  $15.6^{\circ}\text{C}.$ ) and it is in consequence of retardation and gravitation that it also occurs at temperatures up to the critical temperature.

Phenomena like those sketched were also obtained by Andrews with mixtures of carbonic acid and nitrogen, by Van der Waals with carbonic acid and hydrochloric acid, and others. Andrews' experiments are the most complete. He noticed great irregularities in the behaviour of his mixtures and thoroughly investigated their cause. He showed how they are explained by imperfect mixing of the



substances and great retardation in the establishment of the equilibrium in the long and narrow experimental tubes. If the mixture is partly liquid and is then compressed to a smaller volume, the pressure will be higher than it should be, and in leaving the mixture for some time at the same volume the quantity of the liquid increases while the pressure diminishes. If we start from a smaller volume and increase the volume the pressure will be too low and rises slowly while some more liquid evaporates. It takes a very long time for these changes to come to an end and it is very difficult without waiting hours at every change of volume to obtain concordant values at diminishing and increasing volume. Similar uncertainty attaches to the determination of the points *b* and *e* and of the critical constants. If the mixture is not homogeneous the critical temperature may be found several degrees too high.

Similar results were obtained by Ramsay and Young working with a mixture of alcohol and ether. Their investigation brings out the influence of retardation and imperfect mixing very strongly.

Some isothermals for mixtures of carbonic acid and sulphurous acid were obtained by Blümcke, but his experiments do not go as far as the critical region. Ansdell studied the condensation and critical point of mixtures of carbonic acid and hydrochloric acid. A number of observations regarding mixtures, especially critical temperatures, were made by Dewar. Unfortunately, several of the results obtained are doubtful in consequence of the influence of imperfect mixing of the substances.

Critical points of mixtures of liquids were determined by Strauss, Pawlewski, G. C. Schmidt, and others. Differences between mixtures and pure substances were not noticed: in fact the method of observation was, as a rule, one which did not allow either of a measurement of the pressure or of a change of volume.

The above remarks show in what way the experimental method had to be improved in order to get definite results independent of any retardation in the establishment of equilibrium. The little iron stirring-rod (if necessary, en-

closed in a small glass tube) which was applied by the writer of this article to obtain definite results at the critical point for so-called pure substances, as described in part i., was really devised for experiments on mixtures. This rod may be moved up and down inside the narrow tubes by an electromagnet which is outside the tube and the heating jacket surrounding it: it accelerates the process of mixing even at very large volumes, and enables one to obtain almost identical readings with diminishing and with increasing volume. But it is especially at smaller volumes and in the critical region that stirring is very effective. The critical phenomena obtained are practically free from retardation due to slow diffusion and differ materially from the phenomena as described by Andrews and others.

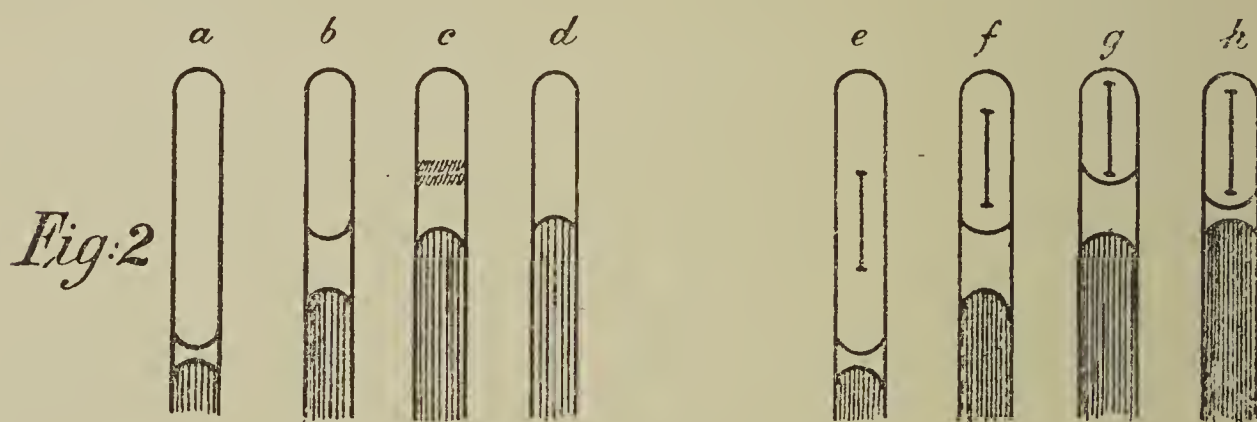


Fig. 2 (*a b c d*) gives the aspect of a tube containing our mixture of  $5/6$   $\text{CO}_2$  and  $1/6$  air at  $18^\circ \text{C.}$  at gradually diminishing volume without stirring as described above. In *a* the condensation has just begun, in *b* the liquid has increased and the liquid surface is flatter, in *c* the quantity of liquid is again more but the liquid surface is just in the act of disappearing (critical phenomenon), in *d* the mixture is homogeneous. Fig. 2 (*e f g h*) shows the behaviour of the same mixture at the same temperature ( $18^\circ \text{C.}$ ) but with stirring; *e* and *f* are very much the same as *a* and *b*, the surface, however, being better defined. In *g* the quantity of liquid *has passed through a maximum and is decreasing* with well-defined surface; in *h* the liquid is nearly all evaporated. No critical phenomenon takes place but a kind of condensation which is called “retrograde condensation” instead. Evidently the same would be found without stirring if one could afford to wait



hours or perhaps even longer. In diminishing the pressure the same phenomena are observed in the opposite order (*h g f e*). The higher the temperature the smaller is the maximum quantity of liquid, and at about  $19^{\circ}$  C. a minute quantity of liquid only just appears but disappears again immediately on compression. Though  $19^{\circ}$  C. may be called the critical temperature, because above  $19^{\circ}$  C. no two phases are possible, no "critical phenomenon" takes place there. If we follow the phenomena at somewhat lower temperature, say  $17^{\circ}$  and  $16^{\circ}$ , we find similar results; but the maximum quantity of liquid increases, while the liquid surface becomes less and less distinct. At last the liquid surface actually disappears, first near the bottom of the tube, and the lower the temperature the higher is the level at which it does so. At  $15.6^{\circ}$  C. it disappears in the middle of the tube, and it is below  $15^{\circ}$  C. that the liquid increases and fills the whole tube before the liquid surface disappears. The critical phenomenon is therefore confined to temperatures between about  $15^{\circ}$  C. and  $16^{\circ}$  C. From the theoretical explanation to be given below it will appear that the critical phenomenon really belongs to one temperature only, in this case  $15.6^{\circ}$  C.; a temperature which we shall denote as  $t_p$ . The fact of its occurrence at a range of temperatures ( $15^{\circ}$ - $16^{\circ}$  C.) is due to gravitation: the explanation is analogous to that given in part i. of the occurrence of the critical phenomenon for pure substances, at different volumes. In this case gravitation not only makes the density different at different levels but also the composition. As  $t_p$  depends on the composition  $x$ , *i.e.*, is different for different mixtures and, therefore, not the same for the mixtures at different levels in the tube, the critical phenomenon does not take place at the temperature  $t_p$  belonging to the mean composition  $x$  (here  $5/6$ ) only, but also at temperatures slightly below and above  $t_p$ , each time at a different level in the tube. The longer the tube the wider the range of temperatures within which the critical phenomenon occurs. All this follows from the theory and is confirmed by experiment. If gravity did not act we should find normal condensation below  $15.6^{\circ}$  C., the critical

phenomenon at  $15.6^{\circ}\text{C.}$  ( $t_p$ ), retrograde condensation with decreasing maximum quantity of liquid from  $15.6^{\circ}\text{C.}$  to  $19^{\circ}\text{C.}$ , and no condensation above  $19^{\circ}\text{C.}$ , the critical temperature  $t_c$ .

The same phenomena have been observed with a number of other mixtures, such as mixtures of carbonic acid and methyl chloride. The interval between  $t_p$  and  $t_c$  is however often much smaller than it was in this case. In mixtures of carbonic acid with acetylene and nitrous oxide with carbonic acid and with ethane the distance  $t_c - t_p$  was so small that no retrograde condensation could be detected at all. These mixtures behave almost like single substances. This result may also partly be due to the action of gravitation which disturbs the real phenomena for mixtures in the way just described.

We are now in a position to complete the  $p-v$  diagram for mixtures and consider in what respects it differs from the same diagram for single substances. The isothermal  $t = 10^{\circ}\text{C.}$  was considered before. The curve shows two breaks at  $b$  and  $e$ : in experiments on mixtures of carbonic acid and sulphurous acid Blümcke found the isothermals continuous even below the critical region; this is due to retardation which tends to blur the discontinuities at  $b$  and  $e$ . On stirring the mixture the discontinuities reappear in the diagram. Through the different points  $b$  and  $e$  belonging to the isothermals at different temperatures we may as before draw a curve, the border or saturation curve. The isothermal for the critical temperature  $t_c$  is then found to touch the border curve, but not as for single substances at the top  $M$  of the border curve but at a point  $C$  to the right of  $M$ . The critical pressure is not the maximum pressure on the border curve. The isothermal for  $t_p$  the temperature at which the mixture shows the critical phenomenon at  $P$  has a shape similar to the shape of the isothermal  $t = 10^{\circ}\text{C.}$  Sometimes  $P$  is found on the left of  $M$ , sometimes on the right, and in exceptional cases it coincides with  $M$ . The isothermals which meet the border curve, must be supposed as for single substances to exist also inside the border curve and the same experimental facts exist to support this hypo-



thesis. Blümcke demonstrated the reality of the so-called theoretical isothermal for a mixture of carbonic acid and sulphurous acid by slowly expanding the mixture when wholly liquid and lowering the pressure below the pressures of the experimental isothermal; and in the same way by compressing the mixture carefully to a pressure above the pressure at  $b$ . The writer of this article has often been able to confirm the former experiment.

The theoretical isothermal is given in fig. 1. as a dotted curve. It changes gradually into the shape above  $t_c$ . For single substances we saw the double wave shape disappear at the top of the border curve (here at M). At this point the critical isothermal for single substances has a horizontal tangent and the isothermals for higher temperatures have no points at which  $\frac{dp}{dv} > 0$ . For mixtures a similar transition takes place but now *inside* the border curve, as may be seen from fig. 1. The isothermals for temperatures just below  $t_c$ , though partly inside the border curve have no unstable part. The critical temperature, as it would be if the mixture remained homogeneous, is below the actual critical temperature.

It will also be noticed that the law for finding the border curve from the set of complete theoretical isothermals must be different from the same as explained for single substances. In that case the Maxwell-Clausius criterion solved the problem. Here the vapour pressure is a quantity which depends on the volume in consequence of the fact that the composition of the two co-existing phases is as a rule different. As was pointed out by Blümcke the area of the two surfaces inclosed between theoretical and actual isothermal must be again equal in this case. But this condition is evidently altogether insufficient for the solution; the complete solution will be given presently.

As regards the continuity of the liquid and vapour states the same remark may evidently be made as for single substances. A mixture in the condition of vapour may be changed into a liquid by a continuous set of changes.

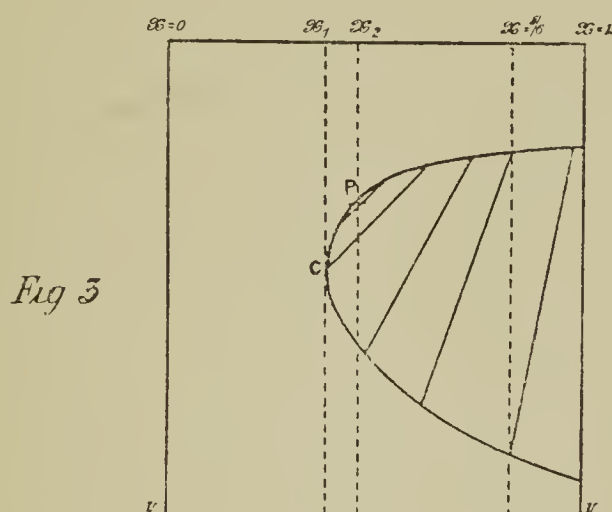
There is no sharp distinction between one and the other any more than for pure substances.

An important question which presents itself is to find co-existing phases. In other words, what is the density (density is the reciprocal of the volume of a given quantity of mixture) and what is the composition of a liquid mixture in equilibrium with a vapour mixture? The liquid which during compression is formed when the condensation begins (at  $b$  fig. 1) has as a rule a different composition (as well as density) from the gas mixture. For our mixture of  $5/6$   $\text{CO}_2$  and  $1/6$  air the liquid will be much richer in  $\text{CO}_2$  and only contain a small admixture of air. During the process of condensation the composition of both phases changes, as a rule in the same direction. For our mixture both the liquid and the vapour become poorer in carbonic acid, richer in air (this is not a misprint!). In the end when the whole of the mixture is changed into liquid its composition is again  $5/6$ , equal to the original composition. Our diagram (fig. 1) only gives us the density of the mixture at  $b$  where it is in equilibrium with a denser phase, a liquid, and  $e$  where the same mixture, but now itself in a denser state, is in equilibrium with a lighter phase, a vapour. But about the second phase, the liquid one which appears at  $b$  on compression and the vapour phase which disappears at  $c$  on compression or reappears on increasing the volume, the diagram does not say anything. We may find those phases however by combining the diagram with those for other mixtures of the same two substances. It is a result of thermodynamics, confirmed by experiment, that at given temperature and pressure there is only one equilibrium of two phases for a mixture of two given substances. The relative quantities of the two phases may be anything, but provided  $t$  and  $p$  do not change, the density and composition are always the same. Suppose therefore we take the isothermals for the same temperature (say  $10^\circ\text{C}.$ ) for a number of mixtures of  $\text{CO}_2$  and air and select that mixture  $x^1$  for which the pressure at the point  $e$ , *i.e.* in the liquid state, is equal to the pressure at  $b$  for our mixture. According to the rule given above  $x^1$  will be the mixture which co-exists at  $10^\circ\text{C}.$  with the



mixture  $5/6$ . The density is found at the same time. The same is true in general. We find sets of two mixtures which at the same temperature have the same saturation pressure, the one when liquid, the other when in a state of vapour. We may find in that way a number of pairs of phases which may co-exist, say at  $10^{\circ}\text{C}$ . and at different pressures.

A better insight is obtained by representing graphically the composition and density or volume of these co-existing phases. Fig. 3 gives the diagram thus obtained. The



only values of  $x$  which are possible are those between 0 and 1 and the diagram is therefore enclosed between two parallel  $v$  axes and the  $x$  axis. The diagram is supposed to be drawn for  $10^{\circ}\text{C}$ . A curve is drawn through the co-existing phases and the corresponding pairs are joined by straight lines. To each of them belongs a different pressure. The pressure is lowest near  $x = 1$  where in fact it approaches the saturation pressure of pure carbonic acid. It gets higher and higher towards the left hand side. The corresponding phases approach each other and finally coincide at  $P$ .

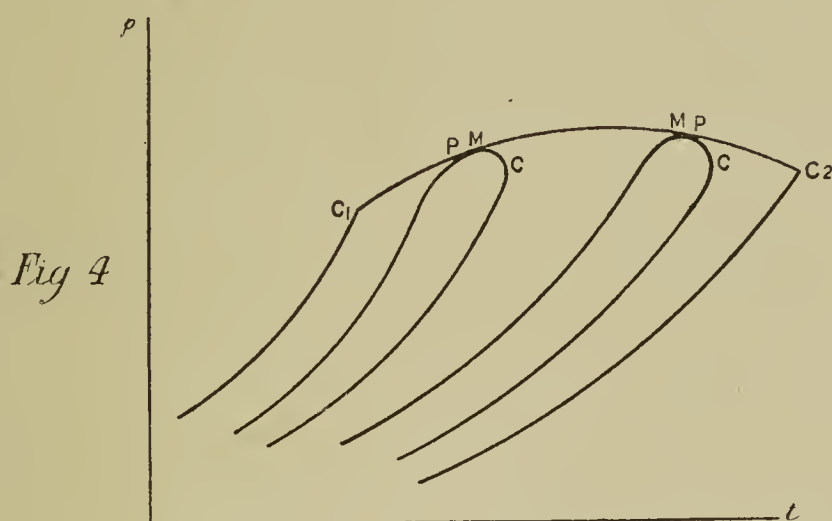
We may read the behaviour of any mixture of  $\text{CO}_2$  and air at  $10^{\circ}\text{C}$ . from fig. 3 as far as condensation is concerned. A mixture for which  $x = 5/6$  when compressed, *i.e.*, the total volume diminishing, shows liquid at  $b$ . The density and composition of this liquid is given by point  $c$ ; on being further compressed the two phases change. The straight line must be imagined to move towards the left and it may be proved that the relative quantities of vapour and liquid

present are given by the ratio of the parts into which  $b_c$  is divided by the stationary vertical line  $x = 5/6$ . The quantity of liquid increases until in  $e$  the whole mixture is liquid. Similar phenomena would be displayed by other mixtures. When, however, the composition  $x$  is less than  $x_1$  (the line  $x_1$  touches the curve in C) no condensation takes place. And for mixtures between the limits  $x = x_1$  and  $x = x_2$  (the line  $x_2$  passes through P) the condensation will be found to be retrograde, the quantity of liquid reaching a maximum and diminishing until it is all evaporated. Mixture  $x_1$  has its critical point in C, and  $10^\circ \text{C}$ . would therefore be the critical temperature for this mixture. Co-existence of two phases which approach each other and finally become identical must give rise to what was called the critical phenomenon and we see that at  $10^\circ \text{C}$ . this would take place for mixture  $x_2$ . In order to return to the phenomena for a given mixture at different temperatures we have to draw the same diagram for those temperatures. It will then easily be seen that the phenomena obtained are exactly those which were described in the beginning. It is found that the critical phenomenon belongs to the one temperature  $t_p$  only if we do not take gravitation into account. In lowering the temperature the curve moves towards the left and at the critical temperature of air would touch the line  $x = 0$ . Below that temperature all mixtures would be condensable and no critical phenomena would exist.

Another instructive way of representing the experimental results is obtained by drawing the border-curves for the different mixtures in the  $p$ - $t$  diagram (fig. 4), first studied by Duhem. The border curves have the shape of loops, in the simplest case lying in between the vapour-pressure curves for the two components. A curve may be drawn enveloping the loops. The points of contact P correspond to P in fig. 1 and fig. 3. The points C where the loop has a vertical tangent also correspond to the points C in figs. 1 and 3. The highest points of the loops (M) correspond to M in fig. 1. The difference between C P and M is clearly brought out by this diagram.



On the left hand side of the diagram  $P$  is to the left of  $M$ , on the right hand side  $P$  is to the right of  $M$  between  $M$  and  $C$ . But evidently  $t_c$  is always higher than  $t_p$  and  $t_m$ ; even when  $P$  lies beyond  $C$  on the lower branch of the loop as is sometimes the case.



By means of a diagram like fig. 4 we may predict with some certainty what the influence will be of an admixture of a substance  $a$  on another substance  $b$ . If the vapour pressure curve for  $a$  is above the vapour pressure curve for  $b$  the vapour pressure is likely to be raised by the admixture. We should also be able to say something of the influence on the critical constants,  $t$  and  $p$ , if we were able to enunciate a rule about the position and shape of the enveloping curve  $C_1 P C_2$ . This however is not the case. The critical temperature of a mixture is, as a rule, between those for the components, but the critical pressure has a tendency to be high for the mixtures and is often higher than for the pure substances. But both these rules, as also the rule that the loops lie inside the vapour-pressure curves, are far from general. The pressures for the mixture are in some cases higher, and in others lower than the vapour pressures for the components. Mixtures of this kind have been investigated by Konowalow, Guthrie, and others. The writer of this article found a maximum vapour pressure for mixtures of  $N_2O$  and  $C_2 H_6$  lying near  $x = 1/5 N_2O$ . This maximum was found to exist up to the critical region for these mixtures. Fig. 4 becomes complicated and, therefore, inconvenient in cases of this kind. As to the critical tempera-

tures, it was long supposed that the critical temperature for a mixture was always between the  $t_c$  temperatures for the components; Pawlewski and Strauss found it to be approximately proportional to the composition. This law does not take into account the difference between  $t_c$  and  $t_p$  and is, moreover, found to be confirmed only in a few instances. Mixtures of  $\text{CO}_2$  and  $\text{CH}_3\text{Cl}$  and of  $\text{CO}_2$  and  $\text{HCl}$  do not obey the law, the deviations being several degrees, and higher for  $t_c$  than for  $t_p$ . Sometimes the critical temperatures for the mixtures are even partly outside those for the constituents. Mixtures of  $\text{N}_2\text{O}$  ( $36^\circ$ ) and  $\text{C}_2\text{H}_6$  ( $32^\circ$ ) containing more than one-tenth of  $\text{C}_2\text{H}_6$  have critical temperatures below  $32^\circ\text{C}$ . There is no reason why more instances should not be discovered, as so few accurate experiments have as yet been made in this direction. The critical pressures were between those for  $\text{N}_2\text{O}$  and  $\text{C}_2\text{H}_6$ . The critical pressures for mixtures of  $\text{CO}_2$  and  $\text{CH}_3\text{Cl}$  are some of them higher than for either of the substances. Evidently there is a great deal of variety. Pictet uses the determination of the critical constants (especially temperature) as a test for the purity of substances. It is obvious from the foregoing that this can only be a trustworthy method in very special cases where the nature of the impurity is known beforehand. A much better, but perhaps somewhat too delicate, test is the constancy of the condensation pressure, though again this method would fail altogether where the mixture was one of maximum or minimum vapour-pressure.

It is now necessary to point out the connection of the experimental results with the theory. In the above I have not followed the historical order. Before any accurate experiments were made, Professor van der Waals published a theory for mixtures without which the phenomena would not have been easily unravelled. It is not inconceivable that most of the results represented by our diagrams might have been arrived at by a long and laborious set of experiments, but practically it was the theory that led the way and even now there is a good deal in the diagrams which depends on the theory and is still waiting for experimental confirmation.



The theory assumes an equation of condition for a mixture analogous to the equation for single substances. Van der Waals uses the same equation for mixtures as he deduced for simple substances, *viz.*  $\left(p + \frac{a}{v^2}\right) (v - b) = RT$  (1) but  $a$  and  $b$  now depend on the composition of the mixture  $x$ . Van der Waals finds

$$a = a_1 (1 - x)^2 + 2 a_{12} x (1 - x) + a_2 x^2$$

and a similar equation for  $b$ ;  $a_1$ ,  $a_2$ ,  $b_1$  and  $b_2$  are the constants for the two components;  $a_{12}$  and  $b_{12}$  depend on the mutual actions. Equation (1) is an equation between  $p$ ,  $v$ ,  $T$  and  $x$ .

Now we may be perfectly assured that this equation is not correct. We saw how even for single substances the same equation fails utterly. But the general results of the theory do not depend on the special form of the equation. We only have to assume, as with single substances, the existence of some equation between  $p$ ,  $v$ ,  $x$  and  $T$  as describing the behaviour of the mixture under different circumstances. This equation should yield an isothermal with the double-wave shape at lower temperatures and no unstable parts at higher temperatures.

It has already been said that Maxwell-Clausius' criterion is not adequate to find the border-curve because of the different composition of the co-existing phases. This criterion was equivalent to the condition that the same number of molecules move from the liquid to the gas in the opposite direction. But as there are two substances the latter condition must now be applied to both. In thermodynamical language this double condition may be combined with the condition of the equality of pressure in the two phases into one condition. Van der Waals uses the condition in this form: in a given volume the free energy  $\psi$  ( $\psi = \epsilon - \tau\eta$ ,  $\epsilon$  = energy,  $\eta$  = entropy) is a minimum. One of the properties of  $\psi$  is  $\frac{\delta\psi}{\delta v} = -p$ .

In the case of one substance  $\psi$  is a function of  $v$  (at constant temperature). Below the critical temperature the  $\psi$   $x$   $v$  curve has a double tangent, the slope of which determines the vapour pressure, the two points of contact re-

presenting the co-existing phases. Points on the  $\psi x v$  curve between those points of contact correspond to points on the theoretical isothermal inside the border curve.

For a mixture  $\psi$  is a function of  $v$  and  $x$  and may be represented by a surface the co-ordinates of which are  $\psi$ ,  $v$  and  $x$ . Van der Waals proves that co-existing phases are now given by a double tangent plane. The surface presents a plait and in rolling over this plait the double tangent plane traces out on the surface the curve which represents the co-existing phases. This curve is called the connodal curve. Points inside this curve on the surface represent unstable or half-stable conditions of the mixtures, analogous to the points inside the border curve. If the corresponding points of contact approach and reach each other on that part of the surface which is inside the two planes  $x = 0$  and  $x = 1$  the plait is said to have a real plait-point; a plait-point is a point at which the co-existing phases become identical. If we project this connodal curve with its plait-point upon the  $v x$  plane we obtain the border curve in the  $v x$  diagram, in other words fig. 3. This diagram appears therefore in an entirely new light. P is now the projection of a plait-point and the curve the projection of a connodal curve. From the meaning of P as a plait-point it is clear that we may expect the critical phenomenon to be characteristic of that point. In general it appears that the study of condensation and critical phenomena may be identified with the study of the shape, position, changes and displacements of plaits and plait-points on the  $\psi v x$  surface.

We are now able to sketch the method by which to find the border curves say in the  $p v$  diagrams for the different mixtures. We must suppose the isothermals of a given temperature for a number of mixtures to have been determined. The equation of an isothermal may be written in the form  $p = f(v)$ . As  $\frac{\delta\psi}{\delta v} = -p$  we can calculate, as is shown by Van der Waals, the  $\psi$  and draw the  $\psi v$  curves for each of the mixtures. These  $\psi v$  curves form together the  $\psi v x$  surface. We then apply the double tangent plane and make it roll over the plait of the surface. The double



curve traced out by the points of contact gives the co-existing phases, and thus the volume at which any of the mixtures will be in equilibrium as a vapour with a liquid, or as a liquid with a vapour. In other words it gives the points  $b$  and  $e$  on the isothermals for the chosen temperature. By doing the same thing at other temperatures the border curves may be traced out in full. The results obtained may then be compared with the border curves, as found by actually observing the volumes and pressures at  $b$  and  $e$ .

A drawback of the  $\psi v x$  surface is the indirect way in which the pressure manifests itself. The pressure depends on the slope of the tangent plane in the  $\psi x$  plane. In general this slope changes continually in one direction during the motion of the tangent plane over the plait, and the maximum pressure is obtained at the plait-point P. This is not in contradiction with the distinction made between the points P (plait-point) and M (point of maximum pressure) in figs. 1 and 4. At M a given mixture has a maximum pressure on the border curve, or above that pressure no condensation is possible for that mixture. P on the other hand is a point of maximum pressure on the plait at a given temperature. At that temperature no mixture can exist in two phases at a higher pressure than belongs to P. But at a different temperature higher pressures may occur unless P and M coincide.

Sometimes the pressure on the plait, instead of rising or falling all the time, passes through a maximum or minimum. This occurs where there is a mixture of constant boiling-point. The co-existing phases have the same composition in that case, though different density, as was first demonstrated by Konowalow. It follows that the straight line connecting the corresponding points on the border-curve (fig. 3) is parallel to the  $v$  axis for that mixture. The straight lines on the two sides of the maximum or minimum line are spread out like a fan; the fan opens out in the direction of the positive  $v$  axis for a minimum, and in the opposite direction for a maximum. The latter case

occurs with nitrous oxide and ethane for a mixture containing about  $1/5$   $N_2O$  and  $4/5$  ethane, as was already stated above. The fact was also mentioned that most of the mixtures of those two gases have critical temperatures below that of ethane. This is entirely explained by a splitting up of the plait before the critical temperature of ethane ( $32^\circ$  C.) is attained, at about  $26^\circ$  C. Each of the halves of the plaits has its plait-point. In one of the halves the plait-point is situated as in fig. 3, *i.e.*, nearer the  $x$  axis than C. But in the other half, opposite the first, P lies farther away from the  $x$  axis than the critical point C. The critical phenomena which one may expect in that case are different from those described in connection with fig. 3. There are again the two temperatures  $t_p$  and  $t_c$ , but between them compression will give rise to the appearance of a second phase lighter than the mixture, therefore at the top of the tube. This vapour phase will first increase and subsequently decrease during compression. This new kind of condensation may be called "retrograde condensation of the second kind". Unfortunately, as was already stated, the temperatures  $t_p$  and  $t_c$  were so close that the critical phenomena were the same as if the mixtures had been single substances.

An important case which has not been considered is that in which the liquid phase itself is split up into two liquids, as in mixtures of water and ether, or water and carbonic acid, in other words the co-existence of two liquid phases and even of three phases, two liquid and one vapour. In cases of that kind the  $\psi$   $v$   $x$  surface has a second plait with properties similar to those of the vapour-liquid plait. If the connodal curves of the two plaits intersect, the tangent plane has three points of contact and therefore three phases will be in equilibrium. At each temperature there is only one pressure at which this triple coexistence is possible, and in the  $p$ - $t$  diagram these corresponding values of  $p$  and  $t$  are represented by a curve. Besides this curve and the two vapour-pressure curves there are the border curves for the mixtures, which in this case have not the simple loop-shape (fig. 4), but form a kind of double loop owing to the



second plait. The theory may predict to a certain extent the various possible cases that may occur, but very little experimental work has as yet been done in this direction. Konowalow and Alexejeff's researches must be mentioned in this connection. Konowalow gives his results as curves in the  $p$   $x$  diagram, Alexejeff uses  $x$   $t$  curves. Both these diagrams are closely connected with the  $p$   $t$  diagram, because all three may be looked upon as sections of, and curves on, a surface, the  $p$   $x$   $t$  surface. We might conveniently call that surface a "border surface" as it contains the phenomena of condensation, including the critical phenomena, for mixtures of two given substances.

The  $p$   $t$   $x$  surface is obviously not the only border surface possible. Any three of the four quantities  $p$   $v$   $t$  and  $x$  may be chosen as co-ordinates for a surface of that kind. A set of  $v$   $x$  border curves (of which fig. 3 is an example) would together give the  $v$   $x$   $t$  border surface, and so on.

The same variety of choice exists if we want to represent by a surface the condition of mixtures when homogeneous, *i.e.* outside (or inside) the border curves. Blümcke has studied the properties of the  $p$   $v$   $x$  surfaces for mixtures. None of these surfaces however gives the co-existing phases by a simple geometrical construction as Van der Waals'  $\psi$  surface does, and as long as the experimental data are so few as they are at present, it is highly advisable to take that surface as a guide and translate as it were its properties into any two or three dimensional diagrams which seem useful for our special purpose.

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J. P. KUENEN.

## A REMARKABLE ANTICIPATION OF MODERN VIEWS ON EVOLUTION.

THE great pioneer of modern anthropological and ethnological research—James Cowles Prichard, was born at Ross, in Herefordshire, 11th February, 1786. The following brief account of his life is taken from Professor E. B. Tylor's article in the *Encyclopædia Britannica* (1885, vol. xix., pp. 722, 723). Prichard was brought up as a member of the Society of Friends, to which body his parents belonged. He joined the medical profession, taking his Doctor's degree at Edinburgh, "afterwards reading for a year at Trinity College, Cambridge, whence, joining the Church of England, he migrated to St. John's College, Oxford, afterwards entering as a gentleman commoner at Trinity College, Oxford, but seeking no degree in either University. In 1810 he settled at Bristol as a physician." Among his many great achievements in anthropology was the proof "that the Celtic nations are allied by language with the Slavonian, German, and Pelasgian (Greek and Latin), thus forming a fourth European branch of the Asiatic stock (which would now be called Indo-European or Aryan)". His treatise on the subject, entitled "*Eastern Origin of the Celtic Nations*," appeared in 1831. "It is remarkable that the essay by Adolphe Pictet, *De l'Affinité des Langues Celtiques avec le Sanscrit*, which was crowned by the French Academy and made its author's reputation, should have been published in 1837 in evident ignorance of the earlier and in some respects stricter investigations of Prichard."

Although Prichard's memory is much honoured, it appears that in one important respect he has not hitherto received his due. My friend Professor Meldola lately drew my attention to a section of the second volume of *Researches into the Physical History of Mankind* (2nd edition, 1826) which, as he pointed out, anticipated in the clearest manner the arguments which have been recently advanced



by Professor Weismann in favour of the non-transmission of acquired characters. The deep significance of the passages in question had been observed by Dr. Maurice Davis, J.P., who brought them under the notice of his son-in-law, Professor Meldola.

In response to Professor Meldola's invitation to prepare an account of this most interesting contribution to the history of evolution, I read the work carefully and soon found that other important ideas are anticipated in it.

Thus, Prichard apprehended with perfect clearness that domesticated races of animals and plants have been produced by the selection of man and not by favourable surroundings, careful training or cultivation. He believed in the possibility of organic evolution and supported it by excellent arguments which still have the strongest weight to-day. He even recognised the operation of natural selection although he assigned to it a subordinate *rôle*. The most important anticipation is, however, the masterly discussion on the transmission of acquired characters, a discussion in which the distinction between acquired and inherent or congenital characters is clearly drawn, and many of the most difficult cases are fully argued out, the conclusions reached being those independently arrived at by Professor Weismann over half a century later.

It is very remarkable that all this should have passed, as I believe, unnoticed. The neglect can only be explained by supposing that this particular edition was never consulted, but that Darwin and others always went to later editions of the same work. I shall be able to show that Prichard was not very confident in the strength of his own conclusions and, so far as I have consulted his later editions and works, I find reason for the belief that his convictions weakened still further. Indeed strong indications of uncertainty are to be found in the second edition itself, although they are confined to the later sections, and do not appear in close proximity to the important conclusions which they nevertheless affect.

It is certain that if Darwin had read this second edition he would have given Prichard a high place in the account

of the history of evolution which appears in the introduction to all later editions of the *Origin*. So too would my friend, Professor Osborn, have given high honour to Prichard in his interesting work, *From the Greeks to Darwin*. It is an anomaly that such works as the *Vestiges* should attract attention, while Prichard's keen insight, sound judgment, and balanced reasoning on many aspects of organic evolution should remain unknown.

I am very far from maintaining that these most interesting anticipations in any way diminish the credit of those recent writers who have treated the same subjects in greater detail and of course independently. The interest evoked by Dr. Davis' discovery in the literature of evolution is mainly due to the work of those recent authors by whom the whole subject has been brought into the light of day, and the attention of every intellectual man and woman has been compelled.

The limits of space oblige me immediately to proceed, after this too brief introduction, with a detailed statement of Prichard's arguments and conclusions, which will be found to justify, in the fullest manner, all that I have said in his praise.

It has already been said that the arguments referred to are found in the *Researches into the Physical History of Mankind*, vol. ii. (London, 2nd edition, 1826). They are included in the seven sections of the first chapter of Book ix (p. 525), which is entitled a "General Survey of the Causes which have Produced Varieties in the Human Species, with Remarks on the Origin of Nations and on the Diversity of Languages". The first chapter treats "Of the Causes which have Given Rise to Varieties in the Human Species". In the first section of the first chapter the author admits that it is fruitless to seek for a complete explanation of the causes which have produced the varieties which are witnessed in the human species. "The origin of the varieties in the breed is enveloped in the same obscurity which still hangs over every question relating to the theory of propagation."

The opinion that the different shades of colour met



with in various races are caused by climatic changes and by varying intensity in the rays of the sun, is then considered, and a great many ancient and modern exponents of this view are quoted. After reproducing a long passage from Buffon, the hypotheses of the Rev. Dr. S. S. Smith of New Jersey are described. These deal not only with the "gradation in the complexion nearly in proportion to the latitude, . . . " but also with the influence which heat exerts upon the secretion of bile. In consequence of heat "the bile . . . is augmented. . . . This liquor tinges the complexion. . . . " "Bile, exposed to the sun and air, is known to change its colour to black—black is, therefore, the tropical hue." This latter and the very similar views of Blumenbach are, however, dismissed by Prichard as "without foundation"; while as to the former suggestion of Dr. Smith, together with that of Buffon and the older writers, he observes that the principal observations on which it is based are correct. "It is certain that the majority of black races of men are inhabitants of the intertropical regions, and that most of the light-coloured nations are to be found in cold or temperate climates." But although he admits the fact, he maintains that it is capable of "a different interpretation from that which modern writers have in general adopted". He similarly admits that the skin of a European is darkened by the sun, and continues: "It seems, at first, not very improbable that individuals darkened by exposure to heat in southern climates, may have an offspring of deeper colour in consequence, and if this effect increases in every generation it may be thought sufficient, in a long course of ages, to produce a black colour of the deepest tint". But this view does not by any means commend itself to him; for he continues "that this notion, however, is altogether incorrect, I venture to conclude from the following considerations:—

"1. The progeny of individuals, embrowned by exposure to the sun, is born with the original complexion, and not with the acquired hue of the parents." Furthermore, he points out that white and black races moved respectively to tropical and temperate climates have retained their original colour for ages. The second consideration which leads him

to reject the above-mentioned conclusion is very significant, and I give it in his own words (p. 532):—

“2. The supposition is contrary to a general law of the animal economy, according to which, acquired varieties are not transmitted from parents to their offspring, but terminate in the generation in which they have taken their rise.”

The succeeding two sections are allotted to the considerations contained in paragraphs 1 and 2.

Section ii. (p. 532) is headed “Instances Showing the Permanency of Complexion in Different Races”. The cases in which races have completely changed in colour after removal to a different climate he explains by a mixture of breed; and points out that “it is easy to find examples of an opposite tendency, and to show that the original hue has been preserved . . . .” Thus he brings forward the instances of the descendants of English colonists in the West Indies and Spanish in South America who “remain as fair as their European ancestors,” when there has been no intermarriage with other races. “That this assertion is correct, I am convinced,” he says, “by the results of repeated inquiries.” In the East the same results are found, although the migration of white races into hot climates took place at far earlier dates. Thus amongst other examples he mentions that of the “white or Jerusalem Jews” who are believed to have migrated to the Malabar coast in the year 490 A.D., and whose living descendants are “said to resemble the European Jews in features and in complexion”.

The converse “experiment of transplanting black races into northern climates” has not been carried on for so long a period, but Dr. Prichard points out that “several generations have produced little or no alteration in the complexion of Negroes in the United States and in other temperate climates”. It is indeed stated that “the domestic Negroes who are protected from the heat of the sun by more clothing, and who pass their time in sheltered houses, are of a darker complexion than the slaves who labour half naked in the fields”.

Section iii. This most significant and remarkable part



of the work is headed (p. 536), "Laws of the Animal Economy in Regard to the Hereditary Transmission of Peculiarities of Structure"; the brief title at the head of the pages runs "Laws of Nature in Hereditary Transmission". This discussion, which forestalls by more than half a century the considerations and conclusions of recent writers and especially of Professor Weismann, is opened by the statement that physiological writers have often inquired "what peculiarities of structure are liable to be transmitted by parents to their offspring, and what terminate with the individual without affecting the race. Perhaps the following remark," the author goes on to say, "may afford the solution of this inquiry".

I must now quote without any omission the succeeding two paragraphs in which the two classes of characters—*inherent* and *acquired*—are defined, as fully and clearly as they have ever been, and the opinion is strongly expressed that the former are transmissible, the latter non-transmissible by heredity:—

"It appears to be a general fact, that all connate varieties of structure, or peculiarities which are congenital, or which form a part of the natural constitution impressed on an individual from his birth, or rather from the commencement of his organization, whether they happen to descend to him from a long inheritance, or to spring up for the first time in his own person—for this is perhaps altogether indifferent—are apt to re-appear in his offspring. It may be said, in other words, that the organization of the offspring is always modelled according to the type of the original structure of the parent."

"On the other hand, changes produced by external causes in the appearance or constitution of the individual are temporary, and, in general, acquired characters are transient; they terminate with the individual, and have no influence on the progeny."

At this point the author adds a most interesting footnote in which he tells us (p. 537) that "this distinction, which has not been pointed out by any former writer on physiological subjects, was first suggested to me in conversa-

tion many years ago by Mr. Benjamin Grainger, of Derby". It would be of high interest to ascertain something more about Mr. Grainger and to find out whether he ever published on his own account. It is however probable, from the other pregnant ideas contained in Dr. Prichard's work, that the clear expression, apt illustration, and admirable discussion of these principles are entirely original.

He then proceeds to illustrate the first proposition "that all original or connate peculiarities of body are hereditary"; first instancing the well-known "porcupine family, in which a remarkable peculiarity of the [human] skin was transmitted through three successive generations," and the facts which prove the hereditary nature of complexion, as shown in section ii. Supernumerary and abnormally thickened digits are then brought forward and proved by many examples to be markedly hereditary; as also "a singular thickness of the upper lip, in the Imperial house of Austria," introduced it is believed "many centuries ago . . . by an intermarriage with the ancient house of Jagellon".

The last examples of such connate characters are especially significant. "The same observation equally applies to those minute varieties of organization, which give rise to peculiarities of habit or temperament, and predispose to a variety of morbid affections, as deafness, scrofulous complaints, and the whole catalogue of disorders in the nervous system. Even those singular peculiarities termed idiosyncrasies are often hereditary, as in the instance of a remarkable susceptibility of the action of particular medicines, such as mercury."

With regard to the second proposition "that acquired peculiarities, or characters impressed by adventitious circumstances, and not arising in the spontaneous development of the bodily structure, are never transmitted . . ." he remarks, as it has often been insisted upon since, that the conclusion "is more difficult to establish than the foregoing . . ., since the proofs must needs be of a negative kind. But," he continues, "there is no want of evidence of this description." And he again insists, as if he could not put it



too clearly and emphatically : “ It seems to be the law of the animal economy, that the organization of the offspring, which as we have seen follows the type given by the natural and original structure of the parent, is unaffected by any change the latter may have undergone, and uninfluenced by any new state it may have acquired ”.

He then discusses the examples which are supposed to support the opposite conclusion, first mentioning the statement “ that dogs and cats, the tails of which had been cut off, sometimes produce young ones which have a natural defect of the same part. It is taken for granted that these appearances are connected together in the relation of cause and effect, and therefore afford a proof that acquired peculiarities are hereditary.” The author argues that cases of this kind are accidental, and he points out that such defect of parts is apt to occur in every species ;—in man as well as in animals. He points to the vast experiment due to “ our caprice ” in mutilating the ears and tails of domestic animals, and to the effects of surgical operations upon man. What remarkable results would be witnessed if such changes were hereditary !

Professor Weismann was first led to the same conclusion as Dr. Prichard by constructing a theory of heredity which seemed to him to explain the facts and observations better than any which had been previously proposed. But the theory did not include any mechanism by which the transmission of acquired characters could take place. Professor Weismann, believing that his theory was in the main right, began to inquire for the evidence on which the belief in such transmission is based, and as soon as he commenced his inquiries the evidence broke down in every direction.

With Prichard it was otherwise, for the existing theories seem to have been against him. Thus he argues that his opponents “ seem to have derived their opinion rather from some conjectural theory of generation, than from any facts which have appeared well established ” ; and he goes on to contend that we know so little “ that we are not authorized to reason from any hypothesis on this subject ”.

He next deals with the statement “ that after mutilation or other artificial change has been repeated through many

generations, a sort of habit may be acquired, by which the new state becomes as it were natural, and may thus modify the race". To this he replies that the evidence of such habit could only be obtained by diminishing the mutilation in progressive generations and comparing the result; whereas in all such cases the violence committed and the resulting injuries are continued unabated. "If, however, an experiment be wanting to prove that repetition effects no difference in the results," he points to the practice of circumcision which has gone on for some thousands of years without producing any hereditary change.

Prichard argues that such non-transmission is beneficial, in fact he contends "that all the laws of nature, or the general plans which we trace through the organized world, tend uniformly to produce beneficial effects, though *particular* evils are sometimes *contingent* upon their operation". With regard to this instance he points out that, if such transmission took place, both man and animals would practically become more and more "mutilated and defective".

The author next proceeds to consider the effects of disease, introducing the subject in the following paragraph: "we cannot discern any essential circumstance in which changes produced by art or by casual injury differ from those which are effected by other external causes. We should therefore suppose from analogy that the latter are not more communicable to posterity than the former, and this presumption is confirmed when we inquire into facts."

He points out that the constitutional effects of many diseases ("small-pox, measles, scarlatina, whooping-cough"), rendering those who have suffered from them more or less immune, are never hereditary. Without attempting to explain in what the change consists, he rightly claims it as "a permanent state of the constitution, which lasts as long as the individual. . . . Those imperceptible modifications in the bodily structure which render the constitution incapable of being acted upon by certain morbid poisons are governed by the same law, as far as regards hereditary descent, as the observable changes of form which are induced by art or accident."



At this point the writer intercalates another clear statement of the essential distinction between inherent hereditary and acquired non-hereditary characters. The statement is so admirable that I quote it in full.

“We may remark in general that each individual being, through the animal and vegetable worlds, has certain laws of organization impressed upon its original germ; according to which the future development of its structure is destined to take place. These inbred or spontaneous tendencies, governing the future evolution of the bodily fabric, cause it to assume certain qualities of form and texture at different periods of growth. From these predispositions are derived the characteristic differences, and the peculiarities of individual beings. Now it appears that such spontaneous tendencies are alone hereditary, and that whatever changes of organization are superinduced by external circumstances, and are foreign to the character of structure impressed upon the original stamina, cease with the individual, and have no influence on the race.”

“Yet this law of hereditary conformation exists with a certain latitude or sphere of variety, but whatever varieties are produced in the race, have their beginning in the original structure of some particular ovum or germ, and not in any qualities superinduced by external causes in the progress of its development.”

These sentences might well have been written to-day, to sum up the results of all our observations on such subjects. These results have been summed up at greater length and in more technical language, but I venture to think that Dr. Prichard's statement contains everything that is valuable and essential in every later attempt. It will be observed that Weismann's conception of inherent characters as blastogenic, acquired as somatogenic, stands out clear and distinct; furthermore, that the source of individual difference is traced to the germ.

After these general statements he returns to the question of disease and discusses predisposition. He points out that medical writers have generally believed that any predisposition to disease may arise in any constitution if subjected to

the appropriate causes ; “that . . . the gouty diathesis, for example, may be acquired by long habits of intemperance, and transmitted to posterity,” and so also with other ill effects witnessed in the children of dissolute parents. If this be so, Prichard admits that “we have a clear proof of the hereditary nature of acquired states of the constitution”.

Against such a view he contends that any particular disease can only follow when there exists “a preparation, laid in the first place by nature, in the original stamina and habit of the body” ; and he points out that the same hurtful cause may produce quite distinct diseases. Thus “intemperate living . . . is commonly said to bring on, in one person, a predisposition to gout, in another to diseases of the liver, or of the stomach, or of the brain. Now since the difference is not in the external causes, it must be in the natural peculiarities of the constitutions on which they act. These, therefore, are previously fitted by original organization to take on them one form of morbid affection rather than another. It is then clear that the predisposition is laid by natural or congenital structure, in the first instance.” Individuals differ in particular organs ; the exciting causes of disease bring out the weaknesses which previously existed and might otherwise have remained unknown. Such defects “being a part of the original bodily structure” are hereditary. “The first individual who exposes himself to the morbid causes, first betrays the peculiar defect of his race, and is thus erroneously supposed to lay the foundation for it.”

Syphilis, which appears to be an exception, he explains by “a peculiar mode of infection. . . . This is evidently a phænomenon of a very different kind from the similarity of structure which the laws of nature have ordained between parents and their offspring.”

Hence he infers “that the phænomena of predisposition to diseases, rather confirms than invalidates the general observations before laid down, and we may be allowed to conclude, that no acquired varieties of constitution become hereditary, or in any manner affect the race”.



The preservation of complexion after a race has migrated to a very different climate conforms to the general law. Although the parents may alter greatly “the adventitious colour has no influence on the offspring”.

Hence in looking for the causes of varieties of mankind we must not “direct our attention to the class of external powers which produce changes on individuals in their own persons, but to those more important causes, which acting on the parents, so influence them that they produce an offspring endowed with certain peculiar characters, which characters, according to the law of nature, become hereditary, and thus modify the race”.

The sentence I have last quoted concludes the section and very naturally introduces section iv., entitled, “Theory of the Origin of Varieties” (p. 548).

This section opens with a sentence which might well have been written by Darwin: “Varieties of form or colour, as they spring up in any race, are commonly called accidental, a term only expressive of our ignorance as to the causes which give rise to them”. On the other hand—“*how, by what influence, and in what manner*” they are produced, “we shall perhaps never be able to ascertain”.

Examples of new varieties which have sprung up within the experience of man are then given: the “porcupine” and six-fingered man, albinos and variations in colour. He next describes the sudden origin of the ancon or otter breed of sheep, quoting from Col. Humphries in the *Philosophical Transactions* for 1813 (part i.).

Prichard favours the view that when the offspring does not exhibit a new variety but follows the main lines of its race or breed, it is apt to be influenced by the father rather than the mother; and he quotes a number of statements and opinions believed to favour this view; and finally alludes to the celebrated cross between the mare and the male quagga in which it was confidently believed that so great an effect was produced on the former that her later offspring, although begotten by a stallion, were influenced in the direction of the quagga (telegony).

The mother, on the other hand, was believed to be in

the main responsible for the new varieties which arise from time to time. This opinion Prichard considered to be probably well grounded; and the conclusion that size and stature chiefly depend on the mother he also thought to be well established. Hence we see that his judgment and penetration were not always proof against popular convictions insufficiently sustained by evidence. These strange views about the relative importance of the two parents seem to have disappeared, and only traces of them are to be found in the popular beliefs of the day.

The author dismisses the extreme cases of the supposed effect of the mother's imagination upon the unborn child as manifestly absurd; but looks with some favour upon the opinion, also held by Erasmus Darwin whom he quotes, that the future offspring may be effected by the imagination of the parent at the moment of conception. In proof of the ancient origin of this belief he alludes to Jacob's experiments upon the flocks of Laban.

When, however, Prichard comes to reconsider all his suggested causes of variation he is dissatisfied with them and admits that "the circumstances—are of a more permanent nature," and that it is often "impossible to discover any peculiar circumstance in the condition of the mother". This leads him to consider the similar instances among domestic animals and among plants and at this point he anticipates in a truly remarkable manner Darwin's general conclusions as to the origin of our domestic breeds.

"It is generally supposed," he says on page 557, "that cultivation is the most productive cause of varieties in the kind, both in the animal and vegetable kingdom. But it may be questioned, does cultivation actually give rise to entirely new varieties, or does it only foster and propagate those which have sprung up naturally, or as it is termed accidentally?"

"In this latter way the influence of art is very important in constituting breeds, as of cattle, dogs, horses. The artificial process consists in a careful selection of those individual animals which happen to be possessed, in a greater degree than the generality, of any particular characters



which it is desirable to perpetuate. These are kept for the propagation of the stock, and a repeated attention is paid to the same circumstances, till, the effect continually increasing, a particular figure, colour, proportion of limbs, or any other attainable quality, is established in the race, and the uniformity of the breed is afterwards maintained by removing from it any new variety which may casually spring up in it."

The main result of Darwin's indefatigable labours on the formation of domestic races could not be more accurately summarised than in these words published in 1826.

Prichard expresses himself as uncertain whether domestic animals are more prone to vary than others, but considers that the artificial conditions may in all probability "occasion deviations in their progeny".

The influence of climate seemed to him the most important of all causes of race-formation—so important in fact that he discusses its examples under a separate section, while the adaptation of races, animal and human, to their climates form the subjects of the concluding sections vi. and vii.

The examples of the effect of climate are brought forward in section v. (p. 558), entitled, "Instances of Variety in the Breed, Arising from the Operation of External, Chiefly of Local Causes". The first instance is that of the swine of Cuba which are said to be twice the size of the parent breed. He then instances the peculiar and uniform colour of the cattle and horses "descended from the variegated domestic breeds" which have become wild in South America, and the common bear which differs in colour in various European localities.

When the races of several distinct species resemble each other in a single locality it is fairly maintained that some special local influence may be strongly inferred. Thus it is stated that the Angora breeds of rabbits, goats, and cats are remarkable for their long fine silky hair and white colour. "These characters . . . indicate a common cause, which must be some peculiarity in the circumstances under which these animals exist in the climate and situation occupied by them."

Then follow many other examples—the blackness which characterises both men and animals in Malabar and Guinea, the whiteness of Polar animals, the height of Patagonian man, the differences which separate the English race in America and the West Indian Islands from that in the parent country, and the negroes of America from those of Africa.

The section concludes in a significant paragraph in which the author suggests that perhaps some of these local varieties may be specially adapted to “the circumstances of the countries in which the deviation has taken rise,” and he finally concludes by introducing the succeeding section in these words: “It may indeed be inquired, whether the deviations in general, which appear to follow a change of climate, are not founded on a law of the animal economy, which gives rise to an alteration in the breed calculated to fit the race for its new abode” (page 566).

The sixth section (p. 567) is headed “Adaptation of Certain Breeds to Particular Local Circumstances”. In this section we are provided with numerous instances of the adaptation of races to their environments. Blumenbach’s opinion in favour of the multiple origin of the dog is quoted at some length. Considering the undoubted adaptation of many breeds for certain ends this naturalist concludes: “I can scarcely persuade myself to look upon this as a mere accidental consequence of degeneration, and not rather as an intentional contrivance of the wise Creator”. To this Prichard replies that such a remark “suggests the inquiry whether the degeneration or variation of animals is in fact a mere accidental phænomenon . . .”. We should note that degeneration is here used in the sense of departure from ancestral type, and not implying, as it does in our time, any degradation or simplification of structure.

Then follows a paragraph most significant of modern views of organic evolution and the kind of evidence on which the modern naturalist relies. The remarkable “double relation” which individual species bear on the one hand to their special localities, and on the other to the group to which they belong, is first pointed out, and main-



tained to be characteristic of the vegetable kingdom as well as the animal. Thus the species of a family or genus are often distributed round a centre "which seems to be the principal focus or favourite seat of the tribe," from which the branches diverge in various directions. The particular species, when compared, can be referred to "one type of organization". The slighter differences between them "seem to lose themselves in the sameness of form belonging to the genus, and even suggest a suspicion that they all proceeded from one original. The phænomena of resemblance must have had their sufficient reason as well as those of diversity." He then inquires whether the explanation is to be found in the action of "some slight modification in the productive causes" which stamped the genus at its first appearance "with all these specific diversities"; or whether on the other hand a uniform genus was first created which "afterwards became diversified by the influence of external agents". He concludes that the former of these alternatives is more strongly indicated by the knowledge of his time.

"Whichever of these suppositions may be true in point of fact, the separation of families and genera into particular species, and the distribution of these species to particular habitations, according to their physical properties, is evidently a part of the provision of nature for replenishing the earth with organized inhabitants, placed everywhere according to the congruity of soils and temperatures, with their structure and habitudes.

"But why is it to be supposed that the influence of this law of adaptation has stopped here? Is it not probable that the varieties which spring up within the limits of particular species, are further adaptations of structure to the circumstances under which the tribe is destined to exist? Varieties branch out from the common form of a species, just as the forms of species deviate from the common type of a genus. Why should the one class of phenomena be without end or utility, a mere effect of contingency or chance, more than the other?

"There are indeed many instances in which we can

perceive an advantage in the varieties of form, and an adaptation of particular breeds to external circumstances." He then gives numerous examples—the small active cattle and horses which are found in mountainous countries, the larger forms which flourish on fertile plains; the various breeds of the hog which are believed to hold "a particular relation to the localities in which they are placed"; the change of a thick fleece into a thin coat when certain breeds of sheep are transported to the tropics. "On considering these and analogous phenomena, we can scarcely avoid concluding that the variation of animals proceeds according to certain laws, by which the structure is adapted to the necessity of local circumstances."

This statement looks at first sight very much like natural selection. It is clear however that the writer held a view similar to that which has been termed "self-adaptation" by some modern writers, *viz.*, that external influences act on the organism in such a manner as to evoke directly a favourable response.

Examples of similar adaptation are then found among the races of man. The skin of black races is considered to be a protection against the effect of heat; the native African races can multiply in localities where a white population cannot maintain its numbers, while negroes are unable to establish themselves in northern latitudes. From these and many other instances, it appears that "in mankind, as in some other races, particular varieties are adapted by constitution and physical peculiarities to particular local situations".

The section finally concludes with the following paragraph: "These remarks, if they are well founded, serve to illustrate the doctrine of variation, or deviation, in the races of animals in general, and they seem to lead us to the conclusion, that this is not merely an accidental phænomenon, but a part of the provision of nature for furnishing to each region an appropriate stock of inhabitants, or for modifying the structure and constitution of species, in such a way as to produce races fitted for each mode and condition of existence. A great part of this plan of local adaptation appears to have been accomplished by the original modifi-



cation of a genus into a variety of species. It has been further continued, and the same end promoted, by the ramification of a species into several varieties."

The seventh and last section (p. 575) of this part of the work treats "Of the Relation of Particular Varieties of the Human Species to Climates".

Prichard evidently thought that adaptation of races to climate is especially characteristic of the human species, and must be admitted to hold in certain instances whatever be thought of his hypothesis that "the varieties in the species of animals proceed from a principle in nature, modifying the structure and constitution of races, and adapting them to the physical circumstances under which these races may be destined to exist . . .". He considers that the distribution of the races of men bears "a certain relation to climates," and gives a broad sketch of the geographical arrangement of races in support of this opinion. At the conclusion, after inquiring how it is that "these varieties are developed and preserved in connection with particular climates and differences of local situation," he gives the following very significant answer: "One cause which tends to maintain this relation is obvious. Individuals and families, and even whole colonies, perish and disappear in climates for which they are, by peculiarity of constitution, not adapted. Of this fact proofs have been already mentioned." We have here the undoubted recognition of natural selection, and it is remarkable that a man of such penetration who recognised fully that domestic breeds are due to man's selection, should not have seen in this principle a larger importance and have extended it to the relations of species to each other as well as to their physical environment. Great as Prichard was he did not appreciate the most pressing part of the "struggle for existence".

Prichard furthermore considers it probable that there are local influences which "promote the appearance of those varieties which are best suited to them, or tend to give rise to their production in the breed". He freely admits that this conclusion conflicts with his contention in section ii., that the colour of a race is not permanently

affected by a change of climate, and, he might have added, conflicts equally strongly with his argument in section iii., that acquired characters are not transmitted. However, he is so fascinated by the view of a local influence directly producing adaptation that he throws over much that he had previously argued for in a most convincing manner. Thus he suggests that races of men when removed into another climate may not change because they are defended from the local influences by living in houses, adhering to their old foods, etc., also that the facts about the black and white Jews of Cochin, from which he argued in section ii. that climate produces no permanent effect on the race, may be insufficiently known.

It is strange that one who reasoned so acutely in section iii. did not seem to see that the following view if proved to be true would undermine the whole of the argument: "It may however be true, that particular varieties, once established in the stock, and transmitted for many generations, though originally resulting in a certain degree from the influence of local causes, will nevertheless continue permanent, even long after the race has been removed from the climate in which they originated".

In spite of this logical flaw, which is in itself of much interest, inasmuch as it probably explains the suppression of Prichard's original views in later works, sufficient has been said to prove that the author was one of the most remarkable and clear-sighted of the predecessors of Darwin and Wallace.

E. B. POULTON.



# THE DISEASES OF THE SUGAR-CANE.

## PART I.

**I**N a preceding paper, the present economic position of tropical sugar-growing countries was passed under review. Attention was directed to the unequal conflict taking place between cane sugar and bounty fed beet sugar for the possession of the market of the world. And it was pointed out that the British West Indian Colonies, unsupported by any form of protection, are quite unable to meet the strain, and appear to be on the verge of bankruptcy.

It would have seemed incredible a few years ago that the cane would ever be replaced by its inferior rival, the beet-root. But the latter owes its present predominance in a measure to this very inferiority. The taxing of Colonial sugars gave the beet growers a chance, and all the resources of modern science were brought to bear upon the improvement of their staple. The problems to be solved were mainly botanical and chemical. It was necessary, by careful selection, to obtain varieties with richer juice, and, by improved processes, to extract a maximum of the sugar in this juice. As a result, the beet-root of to-day is little inferior to the cane as a sugar producer, while the processes of extraction and purification are well nigh perfect.

The fate of cane-growers, tied to their old mills, with their 50 per cent. to 60 per cent. extraction, and 40 per cent. to 50 per cent. waste, is certain ; but there is still fight in those equipped with new and improved machinery, worked on a large scale.

2. In view, however, of the successive phases in this great economic struggle, there is a danger of losing sight of facts of another and equally important class. In a great many estates, whether poorly or well equipped as regards machinery, the cane juice is found to be of very inferior quality ; and this becomes more marked as crop proceeds. The quantity of sugar produced from areas of the same size rapidly diminishes as the season advances, and it be-

comes necessary for the machinery to be worked night and day to prevent serious loss. The cause of this decrease is that the canes are infested by animal and vegetable parasites which increase enormously as the canes ripen. It becomes literally a race between the mill and the cane pests as to which shall appropriate the spoils of the fields. Disease is spread abroad in the estates, changing the delicious juicy canes into vinous and putrid masses. Let us glance at the state of the plantations in different parts of the Tropics.

3. Java, one of the largest and most successful of cane-growing countries, is saturated from one end to the other with *Sereh*, a disease which, after years of close study, has much in it still to puzzle the plant-pathologist. As in many other maladies, there are all degrees between perfect health and pronounced disease, and it is difficult to mention any one characteristic symptom. In severe cases, instead of the normal formation of long healthy joints, the plants become stunted, the canes are arrested in their growth and remain short, while the lateral buds, usually flat and "sleeping," swell and grow out. A bush-form is thus arrived at, more or less resembling that of "sereh" the common lemon-grass (*Andropogon Schoenanthus*).<sup>1</sup> The root-system is poorly developed and diseased at the tips; and what food materials find their way into the stem are diverted from the cane to the bursting lateral buds. In such a plant the fibrovascular bundles are seen to be red in colour, especially at the junction of leafsheath and node;<sup>2</sup> the large vessels are filled with gum which contains immense numbers of bacteria. Obviously this must interfere with the water supply; but it seems probable that the bacteria are mere accompaniments of the disease.

It is difficult to form an idea as to the actual loss inflicted on the island by sereh. One writer has calculated that in 1889 the diminution of crops in Mid Java alone represented a loss of two and a half to five million gulden (£200,000 to £400,000?).<sup>3</sup> A more recent estimate, based upon

<sup>1</sup> Krüger (1) p. 126.

<sup>2</sup> Went (1) p. 470.

<sup>3</sup> May.



circulars sent out during 1896, places the annual loss as 4·83 per cent. of the crops (equal to about £220,000?).<sup>1</sup> Besides the sereh, quite a number of parasitic fungi have been described as attacking the leaves and stalks of Java canes, ranging from harmless saprophytes to active and dangerous parasites.<sup>2</sup>

4. The sugar-growing districts of Queensland and New South Wales, although but recently established, have their full share of animal and vegetable parasites. Most destructive of these is the *Gumming*, thus described by the government pathologist.<sup>3</sup> If, as in slight attacks, a "cane" is formed, cavities appear inside the tissues at the top of the stalk, filled with offensive matter, and accompanying the death of the apical tuft of leaves. Where the attack is severe, plants reach the height of one or two feet, and then die back, shooting out again from the base and forming buds half way down the stalk. The vessels, if examined, are found to be full of gum, and this, under high powers is seen to be swarming with bacteria. As a result of careful inoculation experiments, the disease of gumming has been attributed to the bacteria (*Bacillus vasculorum*) which produce the gum and cause the stoppage of the vessels.<sup>4</sup> While offering many points of similarity with sereh, the Australian disease is readily distinguished by the exudation from cut surfaces, of a clear, yellow mucilage which leaves a bright stain on drying. Gumming is also reported as serious in Mauritius<sup>5</sup> and Pernambuco, the sugar-growing province of Brazil.<sup>6</sup> The latest reports show that this bacterial disease has gained a footing in Java, although at present only found in one or two, strictly isolated spots.<sup>7</sup>

5. The cane-fields in the West Indies are being devastated by a parasitic fungus, recently described as *Trichosphaeria Sacchari*,<sup>8</sup> and locally known as the "rind fungus". In this case the plants frequently grow luxuriantly, and fine, stout canes with good joints are formed. As the time for cutting the canes approaches, to the despair of the planter,

<sup>1</sup> *Archief*, p. 612, 1896.

<sup>2</sup> Wakker and Went.

<sup>3</sup> Cobb (1).

<sup>4</sup> Cobb (2).

<sup>5</sup> Boname (1).

<sup>6</sup> *Sugar-Cane*, 1897, xxvi., p. 377.

<sup>7</sup> Went (2).

<sup>8</sup> Massee (1).

discoloured patches appear upon the joints halfway up the stem. The tissues beneath these spots are seen to be red or brown, and are found to have lost their sweet taste. Examination under the microscope shows the cells to be penetrated in all directions by the hyphæ of a fungus. A little later, black eruptions are noticed on various parts of the stem, especially near the tips of the sleeping adventitious roots, which form a zone at the base of each joint. Fine, curled, black threads are emitted at these points. A microscopic examination of these threads reveals countless conidia united together by a mucilaginous matrix. This is the common or *Melanconium* stage of *Trichosphaeria Sacchari*. The disease is particularly harassing because it does not declare itself till the year's agricultural work is done and there is the promise of an abundant harvest. It spreads with incredible rapidity, and the canes, if not immediately cut, fast deteriorate, until, in bad cases, they are not worth the cost of reaping.

6. In all parts of the Tropics, further, there are numerous animal parasites on the canes. It is difficult to give an idea of their numbers or to form an estimate of the damage inflicted by them. Occasionally one of them increases to the proportions of a plague—witness the locusts of the present season in Natal—but their destructiveness just now seems to be secondary to that of the fungoid and bacterial diseases. There remains much to be done before our entomological knowledge of the cane-fields is at all complete. Here and there detailed studies have been commenced; and there seems some prospect of this being continued in East Java, where an entomologist is attached to the Experimental Sugar Station. One author enumerates between sixty and seventy species of insects known by him to be injurious in the Java cane-fields: six beetles, six “borers,” twenty-five other grubs, several grass-hoppers, four thrips, a number of scale-insects, four or five cicadae, etc., etc.<sup>1</sup>

Most formidable in destructive power, and widest in geographical range is the “moth-borer,” *Diatraea saccharalis*

<sup>1</sup> Kobus (1).



Fab. This form, or one closely allied to it, is met with wherever the sugar cane is grown. It is not very easy to give an idea of the injury caused by this caterpillar, which bores its way in all directions in the juicy cane-stalks. In one field, examined by the author in St. Kitts, five-sixths of the crop was destroyed by the *Diatraea*,<sup>1</sup> whereas the total destruction of crops is not unknown.<sup>2</sup> Its numbers may be gauged from the following figures. On the Brangkal Estate in Modjokerto in Java, 300,000 "borer" grubs were collected from the canes in the space of four months; and this does not appear to have been an exceptionally severe attack.<sup>3</sup>

The grub of a beetle, *Sphenophorus obscurus*, originally described as destroying the canes in the Sandwich Islands,<sup>4</sup> has recently appeared in great force in Fiji. The whole damage during 1892 was estimated at 16 per cent. of the crop.<sup>5</sup>

Another beetle, *Apogonia destructor*, which commences its flights during the West Monsoon,<sup>6</sup> does great damage in Java to the roots of the cane plant. Great care is taken in some estates to collect and destroy the mature beetles before the laying of their eggs. In February, 1896, twenty-three million were brought in by the collectors in ten estates; while in March of the same year, seventy-three million were destroyed in twenty-one estates.<sup>7</sup>

The direct effect of these insect attacks is various. In many instances the damage is temporary and the plant survives. In others the vegetative apex or the roots are destroyed and the shoot dries up. In the great majority of cases, however, the injury is probably an indirect one. The wounds made—especially by the stem-borers—serve as a suitable nidus for semi-saprophytic or parasitic fungi which are not able to penetrate the massive cuticle.

7. This apparent liability of the sugar-cane to the attacks of parasitic fungi and insects is not at all surprising. Whenever plants are cultivated on a large scale, diseases

<sup>1</sup> Barber (1), p. 79.

<sup>2</sup> Cockerell (1).

<sup>3</sup> Hein (1).

<sup>4</sup> *Insect Life*, i., 185, 1888.

<sup>5</sup> *Sugar Journal*, p. 183, 1895.

<sup>6</sup> Zehntner (1).

<sup>7</sup> *Archief*, 1896, p. 465.

sooner or later make their appearance. Forms which have been regarded as harmless suddenly assume dangerous parasitism, or those which have hitherto attacked other plants extend their destructive sphere—*e.g.*, *Botrytis cinerea* and the vine. The conditions of cultivated plants render them peculiarly liable to the attacks of enemies. They are grown in large numbers, close together, so that the spread of disease is unchecked. Certain characters are developed in such plants by human selection: such are the great increase in size of parts (turnip root), the increased parenchymatosis of organs (cauliflower), and the accumulation of substances in the cell sap (beetroot, sugar-cane). All of these tend to disturb the equilibrium of a healthy condition. On the other hand, the selection of disease-resisting varieties is not prosecuted until a specific disease arises. It is not surprising then that, when diseases appear, they assume the greatest virulence, and frequently large areas are destroyed in a very small space of time.

The sugar-cane has peculiarities of growth and substance which render it specially liable to such attacks. Instead of the dry stem and soft leaves of most herbaceous plants, it has a juicy stem and tough, dry leaves. Gnawing and burrowing animals eagerly penetrate the hard rind; and free passage is thus offered for the spores of fungi. The mode of propagation of the sugar-cane is vegetative, by the rough and ready method of cutting pieces off the parent shoot; and by this means disease may be readily transmitted. There is no cessation of growth, as in colder climates, where many diseases are thus annually reduced. The plants are grown so close together that no other herb can exist in the fields when the canes have reached a certain age. The sugar-cane has been cultivated for thousands of years: it is not likely that the prevalence of disease is a new phenomenon in the fields; and, as we shall presently see, this is by no means the case. While singularly open to the attacks of parasites, the sugar-cane has great reproductive power. The plant body is divided into joints, each of which is provided with a resting bud, and each bud or eye may develop into a new plant upon



the ruins of the rotting cane. The success or failure of the growing and grown plant appears to depend less on the thickness of its skin, than on the vitality of the parenchymatous sugar-cells of its stem—whether or not they are able to resist the inroads of parasitic fungi when freely exposed to them.

8. The literature of cane diseases is of comparatively recent date, and this literature is probably due as much to the contest with beet as to any marked increase of disease during late years.

We have, unfortunately for our self-esteem, to look to a foreign country, where a little-known language is spoken, for the bulk of the descriptive work of the last ten years—and there was little done in the cane-fields before that time. It has been the enlightened policy of the Dutch planters to attach biologists as well as chemists to their three sugar stations in Java. And, thanks to the well-directed efforts of these investigators, we are to-day in possession of a valuable descriptive literature, which will serve as a basis for the study of sugar-cane diseases.<sup>1</sup>

The Mid-Java Experimental Station has, it is true, ceased to exist; but a series of important papers were published there by Benecke, who also induced Möbius, Migula, Wieler, and other European botanists of note to contribute essays on special subjects for his journal.<sup>2</sup>

From the East-Java Sugar Station a series of papers have been issued by Valeton, Kobus, Wakker and Zehntner.<sup>3</sup> Of the seventy odd pamphlets published at this centre, over one-third are devoted to diseases of cane plants.

We are indebted to the West-Java Station in Kagok-Tegal for papers by van Breda de Haan, Krüger and Went,<sup>4</sup> describing a great number of parasitic fungi, while the late talented artist, Lucassen, has produced some excellent coloured plates of diseased canes.<sup>5</sup>

Not content with establishing these experimental sugar-

<sup>1</sup>Translations of many of these papers are published in *The Sugar-Cane* and abstracts are to be found in *Zeitschrift der Pflanzenkrankheiten*.

<sup>2</sup> Meded. Mid-Java.

<sup>3</sup> Meded. Oost-Java, and later, *Archief*.

<sup>4</sup> Meded. West-Java, and later, *Archief*.

<sup>5</sup> Lucassen (1)

stations, the assembled planters of Java, in 1893, decided to establish a special journal devoted to cane matters, and placed the venture under the able editorship of Dr. Kobus, assisted by a strong editorial committee. The success of the scheme has been phenomenal. In the *Archief voor de Java Suikerindustrie*, as it is called, a series of valuable scientific papers have appeared in rapid succession. The journal has become the official organ of the sugar-stations, and all their publications are now first printed in its pages. The *Archief* forms already a bulky and indispensable addition to our sugar-cane library, and has met with warm eulogies at the hands of the scientific men at the head of the European beet industry. The specially favourable conditions prevailing in Java, coupled with the undoubted energy of the planters, have placed this Dutch island at the head of cane-growing countries.

9. In the British Colonies, as a rule, no officers are specially told off for the study of the sugar-cane and its diseases, and this work has fallen to the lot of Government Analysts and the Directors of Botanical Gardens. The latter officers are saddled with heavy administrative work, and hardly any descriptive work in cane diseases has been produced in their establishments.

The Director of the Royal Gardens, Kew, has to a certain extent supplied this deficiency, and has invoked the aid of specialists, some valuable papers by Michael,<sup>1</sup> Blandford<sup>2</sup> and Massee<sup>3</sup> being the result. In these cases, however, the character of the work has suffered from its having been carried on in England; and many points have been left to be cleared up in the Colonies.

In the Australian Colonies there are government plant pathologists; and a careful study of cane disease has been made from time to time. Among these a specially able summary has been written by the pathologist of New South Wales.<sup>4</sup>

In the absence of leisure for special study, the great mass of the work done in the remaining British Colonies

<sup>1</sup> Michael (1).      <sup>2</sup> Blandford (1).      <sup>3</sup> Massee (1).      <sup>4</sup> Cobb (1).



has been the careful description of the symptoms on the spot and the forwarding of specimens of diseased canes to specialists in the United States and Great Britain for scientific description. Many of these parcels of diseased canes have been examined and reported on at Kew, and some of the reports have been published for general information.<sup>1</sup> Barbados, Trinidad, Antigua, St. Kitts, Demerara, St. Vincent, Jamaica and Mauritius have all been examined with reference to cane diseases ; and in the bulky mass of official reports we have a tolerable enumeration of the more important pests in the Colonies.<sup>2</sup>

As regards British India, a good deal of information of a general character has been collected in the Dictionary of Economic Products.<sup>3</sup>

In this brief survey of the literature of cane diseases, the United States Experimental Stations must not be omitted,<sup>4</sup> although much of their work is inapplicable to tropical countries, because of the presence of a cold season. It is especially noteworthy that the parasitic fungi do not seem to affect the Louisiana canes in any marked degree ; while the various "borers" may be kept in check by special treatment of the plants during winter—a condition of things widely different from the never-ceasing circle of life and growth in the Tropics.

Lastly, the French Colonies, Martinique, Guadeloupe, Reunion and New Caledonia have not added much of value to the elucidation of disease phenomena ; although specimens of canes have occasionally been sent to Paris, and examined and reported on by plant pathologists.<sup>5</sup>

10. One of the most puzzling features in the study of cane diseases is the concurrent presence of different parasites in the canes. It is frequently a very difficult matter to determine the real cause of any disease ; and it is not surprising to find that the opinions of specialists are frequently

<sup>1</sup> See *Kew Bulletin*.

<sup>2</sup> See especially the Publications of the Botanical Departments and Experimental Stations of these Colonies.

<sup>3</sup> Watt (1).

<sup>4</sup> See especially the Bulletins of the Louisiana Sugar Experimental Station.

<sup>5</sup> Prillieux and Delacroix (1).

at variance. To give an example of this, Went has lately described two very distinct cane diseases in Java. One of these he calls the "pine-apple disease," because of the smell of the canes attacked; and he ascribes it to the presence of a fungus which he has named *Thielaviopsis ethacetica*.<sup>1</sup> The other, which he terms "Het Rood Snot," he traces to a totally distinct fungus, *Colletotrichum falcatum*.<sup>2</sup> Massee, examining specimens of diseased canes sent from Barbados and St. Vincent, and experimenting with sugar-cane plants growing in Kew Gardens, has described a parasitic fungus *Trichosphaeria Sacchari* as the cause of the existing West Indian cane disease called the "rind fungus".<sup>3</sup> He further concludes that *Thielaviopsis ethacetica*<sup>4</sup> and *Colletotrichum falcatum*<sup>5</sup> of Went are merely stages in the complicated life-history of *Trichosphaeria Sacchari*. Went in turn points out that *Trichosphaeria Sacchari*, although probably present in Java, is not at all injurious to the canes there and is merely saprophytic on dead canes. He further disagrees with Massee's conclusions as regards the relationship of these fungi, and lays stress upon the perfectly distinct disease symptoms of *Thielaviopsis* and *Colletotrichum* in Java and *Trichosphaeria* in the West Indies.<sup>6</sup>

The many papers during the last ten years dealing with "Sereh" furnish us with another case in point. This disease has been attributed by different authors to the most various circumstances. Worn out lands, unfavourable seasons, deep planting, artificial manure, root worms, parasitic fungi, bacteria and many other causes have been cited. Treub<sup>7</sup> and Soltwedel<sup>8</sup> regard it as a root disease due to Nematodes. Valetton,<sup>9</sup> Krüger<sup>10</sup> and Janse<sup>11</sup> on the other hand regarded the red-coloured fibrovascular bundles as the seat of disease, and the latter especially endeavoured to prove that bacteria played the same rôle in sereh as they do in "gumming".<sup>12</sup> Benecke<sup>13</sup> strenuously opposed this view and called to his aid various European specialists,

<sup>1</sup> Went (3).<sup>2</sup> *Ibid.* (4).<sup>3</sup> Massee (1).<sup>4</sup> *Ibid.* (2).<sup>5</sup> *Ibid.* (3).<sup>6</sup> Went (5) and (6).<sup>7</sup> Treub (1).<sup>8</sup> Soltwedel (1).<sup>9</sup> Valetton (1).<sup>10</sup> Krüger (2).<sup>11</sup> Janse (1).<sup>12</sup> *Ibid.* (2).<sup>13</sup> Meded. Ost.-Java.



including Migula.<sup>1</sup> Went,<sup>2</sup> in a bulky paper, has reopened the whole question. According to him sereh is caused by the combined presence of a leafsheath disease due to a fungus, *Hypocrea (Verticillium) Sacchari*, and a root-disease, bacteria also being incidentally present. It is known that bacteria, which are the cause of so many animal diseases, are not infrequently present in enormous quantities in plant cells without seriously affecting the life of the tissues; and comparatively few diseases in plants can be traced to their action. It is all the more necessary therefore to exercise caution in attributing any disease among plants to their sole agency. An almost exactly similar controversy has recently been raging concerning imputed bacterial diseases of the vine.<sup>3</sup>

11. The great mass of literature so briefly referred to is of quite recent date. This may be due to the gradual extension to the Tropics of the recent biological activity in Europe. As it becomes more difficult to find subjects for investigation in temperate climates, the overwhelming richness of tropical life in subjects of interest is gradually forced upon one. The earlier observers were unacquainted with parasitic fungi, and their works deal mainly with the insect enemies of the cane.<sup>4</sup> On the other hand, the presence of trained botanists in the Java Experimental Sugar Stations has resulted in the description of numerous parasitic fungi not recorded elsewhere. Not only have the most destructive forms been carefully studied, but numerous less important discolorations of stems and leaves have been traced to the presence of hyphæ in the tissues.<sup>5</sup> There is not the least doubt that many of these diseases, or corresponding ones, are present in every sugar-growing country.

A good deal of attention has always been paid to the insect pests in the Java cane-fields, and a zoologist is specially attached to the East Java Experimental Station. We have, therefore, a long series of papers on insects

<sup>1</sup> Migula (1).

<sup>2</sup> Went (1).

<sup>3</sup> Prillieux and Delacroix (2). Mangin (1). Schilberszky (1), etc.

<sup>4</sup> Guilding (1); Westwood (1); Roth (1), etc.

<sup>5</sup> Wakker and Went (1).

attacking the canes.<sup>1</sup> In studying these insects, many of them are found to be severely checked by parasites. As an example let us consider the "moth-borer". Two species of minute egg-destroying *Hymenoptera* have been described from Java—*Chaetosticha nana* and *Ceraphron beneficiens*.<sup>2</sup> Attention had previously been drawn to the fact that, in the West Indies, but for the presence of a minute undescribed species of *Trichogamma* (?) destroying the moth-borers' eggs, it would be next to impossible to grow the sugar-cane.<sup>3</sup> A species of *Mikrogaster* and a *Chalcid* assist in keeping down the moth-borer in New South Wales, attacking respectively the living caterpillar and the pupa.<sup>4</sup> Lastly, a fungus, recently described as *Isaria Barberi*,<sup>5</sup> has been met with attacking the caterpillars of *Diatraea Saccharalis* in the West Indies; and a similar form of "vegetable caterpillar" has been noted in Java.<sup>6</sup>

Wherever diligent search is made plenty of new species are forthcoming; and it is probable that additional forms of disease will be described when the cane-fields of Fiji, Cuba and the Sandwich Islands are more carefully studied. The history of the first observation of the "shot-borer," *xyleborus perforans*,<sup>7</sup> and the "rind fungus," *Trichosphaeria Sacchari*,<sup>8</sup> in the West Indies favours this assumption, in that when once attention was drawn to these diseases they were speedily found to exist over wide areas.

12. In view of these wide-spread disease phenomena it has been asserted that the cane industry is in danger of being wiped out from natural causes, independently of the beet competition; and that disease is much more prevalent than ever before. Certainly the stricken canes are visible enough. But it may well be that, in the former days of good prices, the planter could with equanimity leave the loads of rotten and rat-eaten canes upon the fields, while he cannot afford to lose a single cane to-day. We read that the sugar crop in Antigua was 3382 hogsheads in 1779,

<sup>1</sup> See especially papers by Kobus and Zehntner.      <sup>2</sup> Zehntner (2).

<sup>3</sup> Barber (1), p. 148.

<sup>4</sup> Oliff or Roebela, N.S.W. Appyelt.

<sup>5</sup> Giard (1).

<sup>6</sup> Kobus (1).

<sup>7</sup> Blandford (1).

<sup>8</sup> *Kew Bulletin*, March, 1894.



and 15,102 hogsheads in 1872; while owing to severe droughts in 1770, 1773 and 1778 there were no crops of any kind, and the whole body of negroes were in danger of perishing.<sup>1</sup>

The records of the condition of the cane-fields in the past are very fragmentary. When the sugar-planters were in great prosperity, the remembrance of individual years of failure was quickly obliterated by succeeding plenty. Nevertheless we do read of severe epidemics among the canes: and the majority of these appear to have been much worse than any at the present time. A few instances will suffice:—

It is recorded by Patrick Browne<sup>2</sup> in 1756 of the “*Aphis blight*” that it was “generally pernicious to all plants on which it breeds: it has been some years known to destroy whole fields, nay whole crops of canes. When they are very numerous, people are obliged to burn everything about them, even the most promising plants.”

In 1760 enormous numbers of “*Sugar ants*” (*Formica omnivora*) infested the cane-fields in the French and English West Indies. These caused such devastation that it was deliberated whether Barbados, formerly so flourishing, should not be abandoned. In 1876 the Government of Martinique offered a million of their currency for a remedy against the plague, and the Legislature of Grenada offered £20,000 for the same object.”<sup>3</sup>

In 1771, Samuel Martin<sup>4</sup> wrote concerning the “*Blast*” that it was “probable that the island of Antigua would in time be ruined by this disease”. This latter appears to be similar to the *Aphis* of Patrick Browne. It is occasionally found in Antigua to this day.

In 1814, Lunan<sup>5</sup> complained of the “*Blast*” in Jamaica “which often destroys whole fields of canes, and is caused by myriads of an invisible insect for which no effectual remedy has been found.”

The Mauritius planters were greatly alarmed in 1848 because of the appearance in the fields of enormous

<sup>1</sup> Edwards (1), p. 447.

<sup>2</sup> Browne (1); Morris (1).

<sup>3</sup> Schomburgk (1), p. 643.

<sup>4</sup> Martin.

<sup>5</sup> Lunan (1).

quantities of grubs which tunnelled into the heart of the canes.<sup>1</sup>

We read that the introduction of the Bourbon Cane into India was followed in 1857-8 by such severe diseases that the canes were literally eaten out of the ground; and this valuable variety disappeared altogether from cultivation.<sup>2</sup>

During the same years in Louisiana a similar infestation of grubs appeared which caused great destruction on the Lower Mississippi. The canes broke to pieces in the fields and no reaping was possible.<sup>3</sup>

In the years following 1872 a terrible outbreak of rust appeared in Queensland and practically swept the cane-fields bare.<sup>4</sup> About the same time we read of great epidemics in the Malay Archipelago, Mauritius, the Society Islands and Bahia.<sup>5</sup>

13. In attempting to form a conclusion as to relative abundance of present and past cane diseases, we are thus confronted by many difficulties. Our records of the past are exceedingly incomplete: increased scientific activity has of late years brought to light numbers of new parasites in the cane-fields: in these evil days the planter cannot bear the loss of the hundreds of rotten canes which so regularly litter the fields during the crop, and he becomes clamorous: we are still in ignorance of the causes of many diseases in the canes, and scientific opinion is not unanimous as regards those most studied.

There are many reasons for thinking that the assumed increase in disease during late years is more imagined than real. Taking a general survey, the cane-fields of the world appear to be fairly normal. Java, with all its diseases, seems to have them well in hand. It is principally in our own West Indian possessions, where scientific work is largely discredited, that the wave of disease is rising which threatens to carry away the last survivors in the economic struggle with the beet producers.

14. Our knowledge of the biology of the cane-fields has made rapid strides during recent years, and we are better

<sup>1</sup> Bojer (1); Westwood (1).

<sup>2</sup> Watts (1).

<sup>3</sup> Cockerell (1).

<sup>4</sup> Spon's Encyclopedia.

<sup>5</sup> *Kew Reports*, 1877-8.



able to distinguish the work of different parasites than in the days of the "Blast". It does not seem, with all their variety, that the diseases are more fatal nowadays. In this, and in other respects, the cane epidemics of former days remind one of the "plagues" of the Middle Ages. The list of diseases to which the human frame is liable has been vastly lengthened by the advance of medical science; but the means of fighting them has increased in a much greater degree. The net result is healthier lives: may it be so in the cane-fields too!

It has been said that a healthy human stomach is cholera-proof: and a parallel may again be drawn with healthy cane plants. A cursory examination of the latter is sufficient to convince one that most, if not all, the diseases of past years are present in a subdued form. The Aphis of the "Blast," the "Sugar-Ant" of Barbados, the "Blackblight" and Cuckoospit, even the dreaded "Rust" of Queensland are all at the present moment widely distributed in the cane-fields, but not injuriously so.

On the other hand, just as new and obscure maladies appear at intervals among human beings, there are evidences of incipient parasitism among the cane pests. Saprophytic forms appear to have become parasitic, and feeble parasites have been changed into dangerous and destructive pests. The "Rind-fungus" of the West Indies appears to afford an example of this. *Trichosphaeria Sacchari* is regarded as an undoubted and dangerous parasite in these islands.<sup>1</sup> Although usually requiring a "bore-hole" for its starting point, evidence from Barbados appears to denote that this is not always necessary; for, as crop proceeds, an increasing number of diseased plants are met with which, after the most careful search, reveal no traces of borers.<sup>2</sup> In Queensland the *Trichosphaeria* has been proved by inoculation experiments to be an undoubted parasite,<sup>3</sup> although it is far more abundant as a saprophyte upon the dead pieces of stems and leaves. In Mauritius it is doubtful whether the fungus is parasitic, although fairly

<sup>1</sup> Massee, etc.    <sup>2</sup> Barbados Experimental Station Reports.    <sup>3</sup> Cobb (3).

abundant.<sup>1</sup> In Java, lastly, repeated inoculations have failed to produce any effect, and this fungus is therefore to be regarded as purely saprophytic.<sup>2</sup> There seems to be evidence that this form, belonging, as it does, to a saprophytic alliance, is acquiring parasitism.

It has been advanced that the altered behaviour of the fungus in various parts of the world is due to the different varieties of cane grown there. The determination and formation of resistant varieties is being prosecuted with vigour in many parts of the tropics. The rind-fungus appears to be only parasitic upon the soft, juicy canes of the Bourbon type. The "hard" *Caledonian Queen* and *White Transparent* varieties, even in Antigua, where the *Trichosphaeria* is rampant, are usually successful in resisting it.<sup>3</sup> But the parasite appears to be gaining power. In a certain area in St. Kitts, in which island the *Caledonian Queen* has been largely grown for nearly twenty years, this hardy cane is already severely attacked;<sup>4</sup> while one of the "hardy" varieties is reported to have been cleared out of parts of Martinique by the same disease.<sup>5</sup>

15. Of a similar nature to this incipient parasitism is the occasional change of habit in insects which may cause much destruction in the crops. This may be the case with respect to a small beetle *Xyleborus perforans* which has appeared in incredible numbers in West Indian canes during recent years. The case is interesting because this form was previously described as destroying wine casks, and the change from dry wood to juicy rotting cane is an extreme one.<sup>6</sup>

There appears to be no doubt that such a change of food has been observed in a minute *Tomicine* beetle found in Nevis.<sup>7</sup> This species has been described as *Hypothenemus eruditus*, from its first discovery in the binding of a printed volume, and it has since been found in various dry substances. In Nevis, however, for a short time, its

<sup>1</sup> Boname (1).

<sup>2</sup> Went (5).

<sup>3</sup> This has been frequently noted; see especially Watts (1).

<sup>4</sup> Barber (2), p. 150.

<sup>5</sup>

<sup>6</sup> Blandford (1).

<sup>7</sup> Barber (3) p. 122.



habits completely changed, and it burrowed into the youngest enrolled leaves of the cane shoot, causing a considerable amount of destruction. The case is remarkable in that beetles of this class do not attack the green tissues of plants.<sup>1</sup>

Sereh is known to have existed in Java for years before it assumed its epidemic character.<sup>2</sup> The rind-fungus is generally believed, in the West Indies, to have lived saprophytically on the cane for years before it acquired strength to attack the living cell; and the shot-borer probably lived in the decaying stumps of the tropical forest for many years before its food demands drove it to attack the canes. There are, so to speak, a host of lurking enemies ever ready to assume the offensive if by any means the cane becomes weakened.

16. With these facts before us, we seem to catch a momentary glimpse of a *grand rotation of disease phenomena*. The cane plants are constantly guarding themselves against the parasites attacking them; and many of the former pests, although present in the fields, have lost their parasitic power. Saprophytic forms as constantly acquire power to pass from the dead tissues and attack the living cells beyond; while those already feebly parasitic gain in power till they threaten to sweep all before them. From the few surviving canes again arises a more resistant variety, in its turn to fall a prey to new forms of disease—and so the cycle proceeds.

We may be encouraged if we can adopt this view. The inroads of the present-day pests will, in due course, be checked by natural means, even if the researches of scientific men fail to shield the planters from present ruin.

It is also encouraging to note that the patient application of scientific knowledge is producing results in fighting these diseases. While the West Indian planter has been too often content to fold his hands in resignation or despair, the Java cane growers are reaping the benefit of their more enlightened policy. The cane diseases are

<sup>1</sup> Blandford (2) p. 214.

<sup>2</sup> May (1).

accurately studied, and their causes, where possible, determined. Regular warnings are issued and special laws are passed: and thus alone is it that so terrible a disease as Sereh, although not stamped out, is restricted within reasonable bounds.

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Meded. W. Java, etc. = Mededeelingen van het Proefstation voor Suikerriet in West Java, etc.

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## “WIND-SCORPIONS,” A BRIEF ACCOUNT OF THE GALEODIDÆ.

THE name ‘Wind-scorpion’ is translated from the Arabic. It is applied to a little known but very important group of Arachnids, some genera of which contain individuals that reach a great size, measuring over two inches in length of body. The principal genus (*Galeodes*), which is that best known to the Arabs, is long-legged, very hairy, and so swift of movement that almost every writer who has had personal experience of these Arachnids has recorded his astonishment at the rapidity with which they cover the ground. A writer, in a private letter to Mr. Pocock, says that they look like a piece of thistle-down driven before the wind. There are, however, also short-legged genera, the members of which, although not so rapid, are yet reported to be extremely agile. In one genus the hind legs are said to be specialised for springing.

Pallas was the first European naturalist who recognised the animal as an Arachnid. Apparently on account of its long legs, he thought it was related to the Harvest-men, and called it *Phalangium araneoides*, or the spider-like Phalangium. Its general resemblance to a spider can also be traced in the German names “Scorpion-spinne,” “Giftkanker” (= poison-spider), and even in the more modern “Walzen-spinne”. It was Olivier who constituted it a new genus under the name of “*Galeodes*” (1791, *Encyc. Méthodique*)—a name perhaps referring to the helmet-like plate at the front end of the body. This plate is of such great morphological importance that it is well that it should be emphasised in the name of this group; for though traceable in most Arachnids, it is so conspicuous in the Galeodidæ as to distinguish them from all the other families.

The Galeodidæ do not make webs like the spiders, but hunt their prey in the open, fairly running it down. They feed chiefly on insects, moths, and even hard beetles, and will strike at almost anything that comes in their way,

scorpions, lizards, small mammals and birds. In one region their chief food is said to be the scorpions. A small nocturnal genus in Colorado is reported to hunt bed-bugs. The name given to the order, Solifugæ, refers to the habit of many genera of only appearing at night. Travellers in Asia, for instance, only see them in their tents, racing over their beds after dark has set in. Other genera, however, show no such aversion to daylight. In Santiago they are even said to run about the streets in broad daylight. It is well for the inhabitants that they are measured in millimetres and not in feet or even inches, for anything more terrible than the jaws of these creatures could hardly be imagined.

These formidable and conspicuous limbs consist of a pair of stout pincers arranged side by side, projecting straight out in front of the animal, with sharp, curved points, and toothed in various ways along the inner edges, the whole outer and distal surface of the limb being thickly covered by bristles. One writer speaks of them as the most horrible jaws in the whole animal kingdom, eclipsing even those of the tiger, the crocodile and the shark.

The method of using these weapons has been described as follows: seizing its prey the animal holds tight with one jaw, while it drives the other deeper in, and then holds tight with this one while the former is driven still further in, the two working alternately in a sort of sawing motion cut deeper and deeper into the victim, which is said often to be "completely devoured". This reported complete devouring of the prey is one of the many points that require investigation. It is worth comparing with the fact that spiders leave very little of their victims. The difficulty lies in the fact that the Arachnids, as a rule, take in no solid food at all, merely biting into the victim and then sucking all the juices out of the wound, these being well strained before entering the œsophagus. It has been suggested for the spiders that, in the act of biting, glandular secretions may cause the firmer tissues of their prey, which otherwise could not be sucked in, to deliquesce. Somewhat the same may be true for Galeodes.



Reaching out in front of the jaws, are the next pair of stout, jointed limbs which are remarkable for their length. These wave in the air as if to “interrogate space”. They carry a remarkable and highly developed “smelling” organ, contained in an invagination at their tips. This organ can be protruded and withdrawn, and has given rise to some controversy. In Lichtenstein’s description<sup>1</sup> the keen sense of smell of these hunters was rightly localised here, *i.e.*, in the swollen knob-like ends of these limbs. This view prevailed until Dufour, who seems first to have noticed the protrusion of the sense organs themselves, claimed them as suckers for holding prey. Other more recent observers who have watched the animal climb out of glasses, etc., touching the glass with the tips of these same limbs, have adopted Dufour’s suggestion that they must be suckers to help in climbing. Another observer of the living animal, who was not aware of the presence of any protrusible organ, described the limbs as emitting a phosphorescent flame from their tips on being applied to any object. This appearance is quite explained by the glistening satin-like appearance of the chitin of the organ observable in its protruded condition. After all, the earlier view was the right one.

The mouth of the Wind-scorpion is a very minute aperture at the tip of a beak, which projects from between the bases of the last-mentioned limbs, but is not visible until the jaws have been pulled apart and raised. This beak, which is quite rigid, is evidently forced by the penetrating action of the jaws into the wound. The juices which are sucked out, are strained through an elegant lattice-like sieve which stands out at the tip of the beak, and is constructed out of the fringing bristles. So finely does this sieve strain the food that on one occasion I found moth-scales retained on its outer surface while, here and there, in the intestines of the same animal, a few similar scales were found, evidently sucked in by the strong pumping of the œsophagus, but in each case apparently forming a centre of disturbance to the normal processes of digestion.

<sup>1</sup> Lichtenstein and Herbst, *Naturg. Insecten, Gattungen Solpuga und Phalangium*, Berlin, 1797.

Another question which requires to be established experimentally is the amount of truth there is in the evil reputation which these Arachnids have for inflicting very painful and even dangerous bites. Lichtenstein (*l.c.*) has endeavoured to show that certain passages found in the ancient classics refer to Galeodes. The "mice" which plagued the Philistines (1 Sam. v. vi.) when they captured and kept the "ark of the covenant" must, according to this writer, have been the terrible Galeodes, while the "emerods" with which they were also plagued referred to the sores caused by the bites of these animals, chiefly on the pudenda. Among other arguments in support of this interesting interpretation of the ancient Hebrew story the same author asserts that Galeodes still inflict similar bites either in the same place, especially of females, or on the lips of people or animals sleeping on the ground. Again, a long passage is quoted from Agatharchides to the effect that a populous district on the shores of the Indian ocean was deserted owing to the swarms of these Arachnids that appeared after a very long rainy season.

On the other hand, Olivier disbelieved the awful reports of the Arabs, who were terrified at the sight of the Galeodes which appeared in the tents at night, and who told yarns, each more horrible than the last, as to their dangerous bites. He admitted however that if the animals did bite, with *such* jaws the results would probably be painful. Pallas says that people are bitten "accidentally" by the animals getting under their clothes and relates a few such cases. Dufour also records a case of a man in Algeria being bitten by a Galeodes that got under his clothes. The descriptions given by these two authors of the effects of the bites, the accuracy of which there is no reason to doubt, are enough to account for the exaggerated terror with which these animals are commonly regarded by the natives in the countries where they occur. This is probably the correct view of the case, and is quite in accord, on the one hand, with the statement that the animals are perfectly harmless, and, on the other, with the description of their ferocity when molested.



Before leaving the subject of the results of the bite, it is to be noted that all the early writers assume it to be extremely poisonous; compare, for instance, the German name for *Galeodes*, “Gift-kanker”. Further, the pain and violent inflammation caused can hardly be accounted for except on this assumption. Dufour searched in vain for poison glands such as those well known in the jaws of spiders, and not finding them gave the problem up. The present writer has suggested that the poison may be the result of simple exudation of matter through the setal pores which can be traced along the tips of the pincers. Such matter would be partly excretory, and hence deleterious to living tissues. It would probably be closely allied to that which, in the hypodermal cells, builds up the chitin and supplies material for the bristles. On the other hand, Captain Hutton records<sup>1</sup> the case of a lizard bitten by a *Galeodes*, which entirely recovered in three days, and uses this as an argument against there being any venom transmitted by the bite. Here the matter rests for the present; we know little beyond the facts that there are no poison glands and that the bite nevertheless sets up violent inflammation.

Among other points to be investigated, mention should be made of the marvellous variety of bristles and hairs which cover many parts of the body; the forms and uses of these are well worthy of study. One obvious suggestion is that they are to a large extent protective. After a good meal, the bag-like abdomen of *Galeodes* may be stretched by fluids to such dimensions that the animal can hardly crawl away. At such a time it would form a rich and easily digested nitrogenous morsel for birds and small mammals. One of its characteristic attitudes of defence is to raise its abdomen right over its back, so that that defenceless member may come under the protection of the legs, for it is on the limbs that the most marvellous bristles occur. Among them are certain curious forked hairs which I have suggested may act as buttoned rapiers, safe to the animal itself but

<sup>1</sup> *Ann. and Mag. Nat. Hist.* vol. xii., p. 81, 1843.

dangerous to any larger creature which, snapping it up, might break off the forked end of the bristle and receive a possibly poisonous wound. On the other hand, birds have actually been seen<sup>1</sup> attacking *Galeodes*, although the observations are hardly sufficient to warrant any definite conclusion either way. Here again experiments are very desirable.

The claws of this formidable Arachnid also deserve mention; they are as terrible, in their way, as are the jaws. They are very long and curved, and their tips are movable. A tendon runs up the hollow of the claw and bends the tip, when needed, sharply round. This mechanism enables the claw to be firmly anchored in the body of the victim.

*Galeodes* stridulates when enraged, and possibly also at periods of sexual ripeness. While watching a specimen which, being confined, was in a "positively astounding fury," Pallas heard the screeching sound which the animal made by rubbing its jaws together. As far as I know, there is no record of any one else having heard this sound, but stridulating ridges have recently been discovered by Hensen and claimed as such by him, although he was apparently unaware that the sound produced by them had been heard by Pallas. These ridges do not occur in all species. Both Spiders and Scorpions are now known also to stridulate; the apparatus, however, seems to be different in each group. This somewhat remarkable fact tends to support the view of the present writer that these different Arachnids cannot in any way be deduced from one another, but are separate developments of some common ancestor.

A few of the more noticeable structural features may be briefly mentioned. The enormous jaws differ from those of all the other larger Arachnids in being hinged on to the front lateral edge of the exoskeleton. The hinge has been formed secondarily out of a crumpling and folding of the skin at the side, and is clearly an adaptation to the great size, and to the powerful muscles of these limbs. The chitinous infoldings forming these hinges give rise to the peculiar areas on each side of the "head," which have given

<sup>1</sup> Distant, *Nature*, vol. xlvi. p. 247.



rise to much speculation. Their purely secondary origin is shown in the fact that the folds which mark them off have come between the large median eyes and the lateral eyes, quite displacing the latter.

With regard to the eyes, it was long thought that the Galeodidæ differed from all the other large Arachnids in having no lateral eyes. But as long ago as 1826 lateral eyes were attributed to Galeodes by so great an observer as Johannes Müller.<sup>1</sup> He claimed six eyes, whereas no one else could find more than two. This claim seems generally to have been dismissed by students with astonishment. One pair of the extra four eyes, for instance, could be explained as the tubercular bases of the pair of bristles often found in front of the large eyes; these, with the bristles knocked off, might be mistaken for eyes. The other pair could not be found at all until quite recently, when, in working over sections, the present writer found two pairs of very degenerate lateral eyes in a species of Rhax, and afterwards discovered similar structures in other specimens. They were not found, however, till long after Johannes Müller's apparently utterly erroneous assertion that Galeodes had six eyes had been dismissed and completely forgotten. Having again looked up the original, the present writer has no doubt that the lateral eyes which he thought he was the first to discover had already been noticed and their true nature guessed seventy years ago. They so little resemble eyes, and the position into which they have been forced by the formation of the hinges for the jaws is so unlikely a place for eyes, that there is little wonder that, until the retinæ were actually seen in sections, they were never again recognised.

Upon the last pair of legs occur the “raquet organs” which have also greatly puzzled naturalists. These are fan-shaped structures supported on short stalks, five on each leg. They are purely sensory, and appear to be erectile. The nerve-endings open round their distal edges. The earlier writers justly compared them with the combs

<sup>1</sup> Vergleichende Physiologie des Lichtsinnes.

of the scorpion, although they should more correctly be compared with the teeth of these combs. Both appear to be functionally connected with the reproductive processes, occurring as they do in *Galeodes* just in front of, and in *Scorpio* just behind, the genital aperture.

So little indeed do we know of these animals that there is still no agreement as to the characters of the sexes. How little reliance can be placed upon the earlier records which speak of male and female specimens may be gathered from the fact that until quite recently the large fusiform spermatophores, which often completely fill the genital glands and may even be visible through the skin of spirit specimens, were generally assumed to be eggs. I have seen many specimens with their glands filled with these white glistening spermatophores, and am still uncertain whether they are males waiting to discharge them or females which have received them. It is quite probable that the females receive many more spermatophores than they require. The superfluous ones are said to be devoured by amœboid corpuscles which also dispose of the spermatophoral envelopes [Birula].

The female is said to attack and devour the male as soon as she has received the spermatophores. This conjugal ferocity is, however, somewhat compensated for by maternal tenderness. The females have been watched digging holes in the ground in which the eggs are laid, the eggs being probably stuck together and protected, as in *Thelyphonus*, by a glutinous secretion.<sup>1</sup> The hatched-out young are closely guarded and watched by the mother. The earlier developmental processes themselves are still quite unknown.

How much we yet have to find out about these formidable yet fascinating Arachnids can be gathered from these

<sup>1</sup> This would, doubtless, be comparable with that which sticks the eggs of the Book-scorpions to the abdomen of the parent, and, further, with that which in *Phrynus* forms the cocoon. This coarsely woven cocoon of *Phrynus* leads on to the web-spinning of the Spiders, so that the elaborate nets of these latter for catching prey can be traced back step by step within the Arachnid phylum to the simple beginning still found in *Thelyphonus* and probably in *Galeodes* of protecting the eggs with a glutinous secretion.



few brief notes. Every one who works at them deplors the scantiness of our knowledge. While the Spiders hang out their marvellous webs on every bush, and the Scorpion's sting is a household word, Galeodes has suffered for lack of sufficient advertisement. It is one of the objects of this paper to press home the claims of this family to the attention of naturalists. The collections, even in our largest museums, are very small, and reliable observations on the living animal are scanty in the extreme, and yet I think it will be admitted by my readers that these Arachnids rival both the Spiders and the Scorpions in interest.<sup>1</sup>

But even if our knowledge of the various forms, and the habits of life of the Galeodidæ were far more complete than they are we should still not be satisfied. We can no longer stop at admiration and minute description of existing forms alone. It is now generally recognised that the most stationary of organisms are not really stationary, but are all plastic and variable. They change as the environment changes, responding with exquisite sensitiveness to any alteration in the impact of their material surroundings. Important, perhaps pre-eminent, amongst these varying factors must be reckoned the food supply. It is a firm conviction of the present writer that no other factor has played so large a part in bringing about the multitudinous forms of animal life as the acquirement of new methods of feeding. The bearing of this upon the origin of the Arachnida will be explained more in detail in what follows.

According to the modern view, the Scorpions with all their many though, comparatively speaking, slight variations (for the Scorpion ranks high among the more stationary forms, having varied but little from the type of its Silurian ancestors) represent so many plastic waves which have radiated out from some centre, changing as

<sup>1</sup> I should like to add that the death of a brilliant young American naturalist, J. Duncan Putnam, at the early age of twenty-six deprived this family of an enthusiastic advocate. Putnam, on his first acquaintance with them was fascinated by them, and began to investigate them systematically. Among other studies, he compiled a list of 224 treatises and references in the literature (up to 1881, the date of his death) dealing with these animals; of this number hardly 10 per cent. are original observations.

they went in adaptation to their changing circumstances. Similarly the Spiders, far surpassing the Scorpions in richness and variety of the present forms, have spread over the face of the earth as so many modifications of some ancestral spider. Further, comparison of the general structure of the Spiders and Scorpions shows that their ancestral forms were related, *i.e.*, were themselves variations of some still earlier Arachnidan form which was neither a scorpion nor a spider, but yet gave rise to them both.

A new ideal thus ennobles the science of Zoology. Animal forms are no longer merely minutely described but analysed, and by a careful comparison of the different forms composing a group, the more fundamental features are sifted out from the more superficial variations until we are able to picture to ourselves with more or less accuracy a hypothetical ancestral form which could have given rise to all the existing members of that group.

In this way it ought at first sight to be possible theoretically to reconstruct with some degree of accuracy the form of the original Spider or Scorpion by selecting with care and judgment those characters which are common to all Spiders or Scorpions and which therefore appear to be their common heritage. As a matter of fact, however, the process is not so simple. We cannot hope to arrive at any true idea of the primitive Spider or Scorpion without all the while keeping the other Arachnidan forms, the Book-scorpions, the Pedipalpi, the Galeodidæ and the Mites constantly in sight. A character, for instance, which is present in all Spiders may be so variable that it is not always possible now to determine what its primitive condition was without comparison with the homologous structure in the other Arachnids. I say not "always" possible, because there are adaptations which are so obvious that it is not difficult to decide which is the simpler and primitive and which the more complex and secondary. Practically, therefore, the method of analysing each group separately is not to be recommended. An attempted reconstruction of the primitive Spider requires constant comparison with the other Arachnids.



The two forms which have been most diligently studied in the past have been, as above noted, the Spiders and the Scorpions, with some reference to the large Pedipalpi. The Book-scorpions and the Mites, being smaller forms, have been left somewhat on one side, while the very important claims of the Galeodidæ to a voice in settling the family tree of the Arachnida, although long ago put forward, are only now beginning to be closely examined.

Here, then, is another inducement to collectors and naturalists, not only to make good the deficiencies in our museum collections but also to supply material to our laboratories; for the morphological interest centring in the Galeodidæ is as great, if not greater, than the biological.

I propose, then, as briefly as possible, to describe comparatively some of the special features of the Galeodidæ, in order to show how near they take us to a reconstruction of an ancestral form capable of producing all the known Arachnids.

In all segmented animals, no matter what theory we adopt as to the origin of metamerism, we are justified in assuming that that form which shows the segmented condition least modified and obscured by fusions and distortions of segments remains in this respect nearest the common ancestor of its class. Few animal groups show such a marvellous variety of modifications of the primitive segmentation as the Arachnids. Each family has its own distinct methods and degrees of fusion, and what is most remarkable is that these different fusions seem to be distinct from one another. This is very important because it appears unmistakably to prove, what we have already suggested above, that all the Arachnid families are distinct specialisations of some primitive form, *i.e.*, they cannot be deduced from one another.

These different fusions are worth noting and comparing. Galeodes has the first three segments fused and all the rest free; the sixth and seventh, however, are modified by the constriction between them being drawn in to form a waist. Behind the waist all the ten segments are swelled up to form a bag-like abdomen capable of enormous ex-

pansion. *Schizonotus*, which is a most remarkable but little known form, superficially resembling *Thelyphonus* but with a jointed cephalothorax and the large helmet-plate like *Galeodes*, appears to have the first four segments fused. *Scorpio* has the first six segments fused, and no external trace of any waist, although, internally, the constriction between the sixth and seventh segments has been drawn in to form a diaphragm; all the segments behind the seventh are free. Seven of these are swelled up to form a distensible bag, while the last five show an exactly opposite specialisation; they are thin, drawn out, thickly armoured and firmly hinged to one another to form an almost invulnerable tail, the terminal joint of which is armed with a sting. *Thelyphonus* has the first six segments fused rigidly together so as to form a long narrow cephalothorax, a waist between segments six and seven, nine abdominal segments free and forming a distensible bag, and three minute telescoped segments forming a sort of short tail which carries a long whip-like appendage. *Phrynus* differs from *Thelyphonus* in having the first six fused segments so compressed longitudinally that the cephalothorax is as broad or broader than it is long, while the tail segments are more telescoped and not furnished with any caudal appendage. The Spiders have the first six segments fused into a compact round or oval cephalothorax, a waist between the sixth and seventh segments, and all the abdominal segments fused together. These latter nevertheless form a distensible bag, but not by any means so distensible as in the case of the other Arachnids with freely telescoping abdominal segments. The Book-scorpions have the first five or six segments fused, no waist visible, all the abdominal segments free and forming a distensible bag. The other families, Harvestmen and Mites, departing somewhat far from the leading types here described, need not detain us.

Now, of these various fusions and specialisations of segments *Galeodes*, with only three fused segments, shows far and away the least modification of an assumed freely segmented ancestor. No other Arachnid (except *Schizonotus* and, perhaps, some of the Book-scorpions) has less than six,



while the Spiders have all the segments fused into two compact groups joined together by a waist.

On analysing and comparing these different fusions and modifications of segments, we find three features common to them all. In all at least the first three segments are fused together, and in all there is some trace of a waist between the sixth and seventh segments, and in all the segments immediately behind the waist are capable of distention. In these facts we may therefore find some indication as to what the common ancestral Arachnid was like.

Hitherto, discussions of affinities based upon segmentation have dealt almost entirely with the number of segments. Most of my own work with Arthropods has gone to show that, important as are the fusions of segments treated quantitatively, that is not enough. The segmentation must be studied and compared qualitatively. It is not enough to ascertain merely how many segments are incorporated in each fused area, we must also ascertain how they have been fused together, that is, how distorted in the process, and, where possible, why they were so modified. Some idea of the importance of this qualitative study of segments will be gathered in the following pages.

Now the fact that the Galeodidæ have, alone among Arachnids, retained the primitive number of fused segments, would lead us to expect that they would also show the qualitative nature of this fusion more clearly than any other Arachnid. And this is indeed the case. Careful examination of the relative character and position of the limbs and mouth, compared with what we know of the nature of the food, shows that this primitive fusion and distortion of the segments must have been brought about as an adaptation to a special manner of feeding. What this method of feeding is, we have already described: the first pair of limbs are thrown forward on each side of and above the anteriorly placed mouth; they seize and crush the prey, the blood of which is then sucked out.

If now we can further show that the ancestral Arachnid fed in the main as Galeodes feeds, we should then have

still further light upon the shape of this primitive form, for we should be justified in assuming that the exact method of distortion of the early undifferentiated segments was in the main that which still persists in *Galeodes*. As a matter of fact, then, we do know that the method of feeding of *Galeodes* was the primitive method. All the principal Arachnids still seize and crush their prey with either the first or the first and second limbs, which are thrown forward round the mouth, and the juices are sucked out. I say all the principal Arachnids, for in some of the more specialised groups, the Harvestmen, and the Mites, the type may here and there be departed from. But even in these forms it persists with sufficient frequency to justify us in concluding that this method of feeding was first acquired by the ancestral Arachnid from which all the existing derivative forms must have inherited it. So much indeed we could have arrived at without the assistance of the *Galeodidæ*, but it is doubtful whether we should ever have unravelled the actual mechanical distortion of the segments which led to the initial differentiation of the primitive Arachnid from its more simply annulate ancestors, but for the persistence of a form which has never added to the primitive number of fused segments.

What then was the nature of this primitive distortion of the three anterior segments, so far as we can gather it from the conditions found in *Galeodes*? Our analysis leads to the following conclusions:—

1. The segments were at one time simple annular segments like those along the rest of the body; the mouth opened on the anterior face of the first segment; a large fleshy prostomium or upper lip protruded anteriorly above the mouth; and from the side of each segment a pair of simple limbs, richly covered with bristles, projected laterally. That is this analysis takes us back to a simple Chaetopod Annelid.

2. This simple condition was first departed from by the bringing forward of the first pair of limbs to the sides of and slightly above the mouth. The two limbs, thus arranged side by side at the anterior end of the body, not



only squeezed and depressed the prostomium or upper lip between them but entirely altered the shape of the first segment to which they belonged. The sides of the segment on which they were originally inserted with the surrounding regions to which their muscles were attached must have shifted from their original positions and become the bases of the limbs in their new positions. The lateral regions of the first segment were thus gradually folded upwards over its dorsal surface. In time as the limbs grew in size and strength and required larger and deeper bases, these folds spread backwards over the dorsal surfaces of the second and part of the third segments, the two folds eventually meeting in the middle line, obliterating the old dorsal surface with the exception of one small island which carried the eyes. In all existing Arachnids the lateral folds of the first segment, carrying the first pair of limbs, have met along the middle line, the junction being still marked by a suture through which in many forms the ocular tubercle protrudes; but the fact that a fossil scorpion from the Silurian shows an irregular shaped island of the dorsal surface not yet covered over by these folds makes it doubtful whether they ever actually met in the ancestral form. The meeting may have been a later specialisation of the derived forms.

3. This translocation of the first pair of limbs to a position above the mouth made room for the second pair to come forward also. This they did, and took up positions at the sides of and slightly below the mouth, their coxal joints pointing forwards. In some cases (*e.g.*, *Thelyphonus*) they have fused longitudinally below the mouth just as the basal regions of the first pair fused together above the mouth.

4. The anteriorly placed mouth was thus in time surrounded by limbs, two above and two below, and its shape became specialised accordingly. The prostomium squeezed between the jaws fused along its lateral edges with the edges of the underlip which had been forced to protrude anteriorly by the forward movement of the limbs of the second segment. In this way a sort of rigid beak was

formed, with a small mouth aperture at its anterior end. This beak persists in the Galeodidæ. It is found also in the Book-scorpions, in some Mites, and, though it is here of no further use as a beak, in Thelyphonus. Further, the mouth parts of Scorpions, Spiders and of Phrynus can all be deduced from such a beak by the suppression and modification of different parts. There is thus an abundance of evidence that the mouth in the primitive Arachnid was at the end of a beak in all essentials like that still persisting in Galeodes.

Thus by the aid of the Galeodidæ, the initial distortion of the primitive segmentation which transformed a simple Chætopod into the ancestral Arachnid can be unravelled, while its physiological significance as an adaptation to a new method of feeding is clear. We have now to show how profoundly this initial adaptation modified the whole of the rest of the organisation of the ancestral form and consequently of its derivatives, the existing Arachnids. We must limit ourselves to a few of the more important structural features which can, with every probability, be shown to be concomitant adaptations.

*The waist or diaphragm.*—This constriction, which occurs, as we have seen, in all the larger Arachnids between the sixth and seventh segments, must be regarded as inherited from the primitive form. Its significance is not far to seek. The region anterior to the waist contains the central nervous system and the powerful musculature for moving the proximal joints of the limbs. Now not only does the pumping action of the œsophagus suck in the juices of the prey but, like a force-pump, it drives the liquid food into the alimentary system, distending it to its utmost capacity. This arrangement obviously requires regulating. Undue pressure on the nervous and muscular tissues has to be avoided. Hence we find a general tendency for the alimentary system to lose its lateral branches or cœca in the anterior region, and, compared with its condition in the distensible abdominal region, to be but feebly developed. On the other hand, behind the waist or diaphragm, the alimentary system is enormously developed, and complicated systems of branching diverticula, different



in the different Arachnids, fill up every available corner of the abdomen left free by the circulatory, respiratory and genital systems. Into this richly branched alimentary system the liquid food is pumped to its utmost capacity, and, owing to the diaphragm, without any danger of disturbing the nervous and locomotory systems of the anterior region. Further, there is some anatomical evidence to show that when the abdomen is distended with liquid food the alimentary canal can be constricted as it passes through the waist or diaphragm, as an extra safeguard to prevent the liquid food from flowing back into that portion of the alimentary system which runs through the anterior region.

The habit of distending the abdomen to monstrous proportions with liquid food seems common to all the larger Arachnids. Individual specimens with distended abdomens may of course be gravid females, but as often as not, they are animals which had been killed just after a full meal. The most familiar Arachnid thus distending itself does not, however, happen to be one of the large forms, but a Mite. I refer to the Ticks which, before fastening on to their hosts, are quite insignificant in size, but, when once fixed, suck in so much blood that they swell up to the size of a bean. It seems, indeed, as if their tough skins were as much an adaptation to prevent them from bursting through over-feeding, as to defy the efforts of their hosts to scratch or rub them off.

*The Degeneration of the Abdominal Limbs.*—The differentiation of the body into an anterior locomotory and a posterior vegetative region sharply divided from one another, has led to the degeneration of those limbs which originally belonged to the segments of the posterior region. We have every reason, however, to believe that, in the ancestral form, they long persisted in a more or less useless condition. A few of these aborting limbs have been utilised by the different existing Arachnids, but in very different ways. Those of the first abdominal segment generally persist as protections for the genital aperture, as a rule simplified to a pair of covering scales, but in Harvestmen and certain specimens of *Phrynus* they form distinct

appendages, for there is every reason to believe that the long genital process of the former is really derived from a pair of limbs. The limbs of the second segment persist only as scales covering the apertures of the tracheæ in Galeodes, but in Scorpio they are still more or less leg-like and are specialised as sensory appendages—the “combs”. Further, we have spinnerets, two pairs in the spiders. These are very large and jointed like legs in some forms. And lastly, we have the sting of Scorpio which is perhaps best accounted for as having been formed out of the limbs of the last segment, fused posteriorly over the anus. This would at least account for the *pair* of poison glands with two distinct ducts and apertures.

*Specialisation of the Respiratory Invaginations.*—An interesting problem is presented by the respiratory system of the ancestral Arachnid. What was it? We have at least three distinct types of respiratory cuticular invaginations in existing Arachnids. As the most highly specialised we have what are known as book-lungs, because the air runs in flat spaces separated by chitinous laminæ within which the blood circulates; these are arranged alternately like the leaves of a book. Such localised lungs necessitate a highly organised circulatory system. They are found in Scorpions, Pedipalps and Spiders. A second well-marked kind of respiratory invagination occurs in the Book-scorpions, Harvestmen and some Mites. It is a simple tubular invagination, the inner end of which widens and then breaks up into an enormous number of long fine tubules carrying air into the remotest parts of the body. These are called tuft-tracheæ. Lastly we have the ordinarily branching tracheal tubes which are best developed in the Galeodidæ.

These three forms of respiratory invaginations must certainly be regarded as modifications of some simpler form, from which they could all be derived. I say “must” because they all open in exactly the same association with limbs or limb-vestiges and are thus certainly homologous structures. There can, I think, be little doubt that these different forms of tracheæ are due to the different ways in which the alimentary canal has developed under the influence



of the force-pump action of the œsophagus, for the respiration is always intimately associated with the circulation, and it is this latter that would be affected first of all by any great extension of the alimentary system. This subject would, however, require more details for its elucidation than the limits of this article would permit. I have dealt with it in detail elsewhere.

*The Number of Pairs of Stigmata.*—Although, in existing Arachnida, the respiratory invaginations are now confined in each form to a very few segments (at the most four, Galeodes, Scorpio) we are fully justified in asserting that, in their simple condition in the ancestral form, they were present, one on each limb, throughout the whole extent of the body. Specialisation of this diffuse condition must very early have set in, indeed such limitation must have proceeded concurrently with the differentiation of the body into two regions. The restriction of the digestive and generative processes to the abdomen would tend to confine the circulatory and respiratory mechanisms also to this same region. Hence, we find the respiratory invaginations early disappearing from the anterior region. This disappearance would be still further accelerated by the tendency to knit the whole of the anterior region into a rigid skeletal box specialised purely for the mechanism of locomotion. It is strongly confirmatory of the whole line of argument here used that the only Arachnid (omitting the Mites) which has retained a pair of respiratory invaginations in the anterior region is also the only Arachnid which has never added any segments to the first three, the fusion of which, as we have above endeavoured to show was the initial specialisation which differentiated the class Arachnida from their Annelidan ancestors. In all other existing Arachnids, except in certain Mites, the respiratory invaginations have disappeared entirely from the anterior region.

Those on the abdomen on the other hand seem to have persisted for a long time as a complete series, although here also they early began to degenerate progressively from behind forward, so that they are now only found in a few pairs on the anterior abdominal segments close

behind the genital aperture. This progressive disappearance of posterior stigmata can still be followed in the Galeodidæ, where the whole aspect of the middle line of the abdomen suggests the disappearance of a long series. Three pairs are said to occur in the genus *Datames*.<sup>1</sup> In the genus *Galeodes*, the most posterior of these is degenerated to a single aperture, the tracheal tube to which appears to be aborting and in some cases seems actually closed; while in the genus *Rhax* this last pair has finally disappeared, leaving no trace either of aperture or tube. The reason for this degeneration of the posterior stigmata requires investigation.

In the Book-scorpions there are only two pairs functional with seven pairs of scars which I have claimed as the vestiges of stigmata. In *Thelyphonus*, behind the two functional stigmata, scars are found as far back as the eighth abdominal segment, these scars showing not only traces of the former stigmatic apertures but also of the hard convex scale-like plates to which the limbs associated with the invaginations had been reduced. These plates are very marked in *Scorpio* where they are still functional, and serve no doubt to protect the specialised lung from external pressure.

*The Endoskeleton.*—The remarkable endoskeleton which is a characteristic of the Arachnida, and differs in each form, has been the subject of a considerable amount of discussion. The clue to its right understanding has again been supplied by the Galeodidæ. We gather from the condition of the unfused abdominal segments in the Arachnida that originally, *i.e.*, in the ancestral form, all the harder rings of skin representing the segments were separated by very flexible intersegmental membranes. In the abdominal regions these are utilised in the formation of the collapsable vegetative sac. Between the sixth and seventh segments this membrane has been drawn in to form the waist or diaphragm, while in the region in front of the waist, on the harder rings fusing together to form a rigid cephalothorax, these

<sup>1</sup> According to a figure by Putnam.



membranes were drawn into the body to form an internal skeleton, the shape of which varies according to the ways in which the component segments have coalesced. A comparative study of these endoskeletal structures and the different ways the segments have been knit together shows this beyond dispute. In the Galeodidæ, in which the three posterior segments of the anterior region remain free, the endoskeleton is limited to one single pair of infoldings, *viz.*, of the membrane between the third and fourth rings. What is also important is that in Galeodes this endoskeleton is clearly seen to be nothing but an infolding of the exoskeleton, whereas this origin is now difficult to establish in the cases of the other Arachnids, specialisation having gone so far that the whole structure seems more like a complicated framework of sinewy or tendinous matter than a derivative of the chitinous cuticle by simple infolding. This structure, then, is clearly due to the differentiation of the body into two highly specialised regions.

These, then, are a few of the structural modifications early initiated in the ancestral Arachnid and due to the further specialisation of its adopted method of feeding. These again have been carried further in various directions by the different descendants of that ancestral form, the modern Arachnids. In nearly all cases, it will have been observed, the Galeodidæ have retained the ancestral conditions least changed.

Before summing up these points in order to obtain a rapid outline sketch of the ancestral form as here reconstructed, another point of importance claims our attention. The ancestral form must have been marvellously richly supplied with glands of some simple kind from which the many glands to be found in the Arachnida could be deduced. There are poison glands, glands for sticking the eggs together (cement glands), and glands, the sticky secretion of which, hardening as it is drawn out yields the silk for cocoons and webs, and, lastly, stink glands. That all these are derivatives of some common form of gland is evident to any one who makes a comparative study of them. The

web of the Spiders<sup>1</sup> for instance comes partly from glands which are serial with the cement glands of the Book-scorpions. These again are apparently homologous with the gland supplying the coarse silk for the cocoon of *Phrynus* and the glutinous matter sticking together the eggs of *Thelyphonus*. Again, the web-spinning glands of the Book-scorpions open at the tips of the jaws close to where, in the Spiders, the poison glands open; while the glands of the spinning Mite (*Tetranychus*) open in the corresponding place on the second limbs, and the poison glands of the Scorpion open at the tip of the sting which I regard as a pair of fused limbs (see above). Lastly, the poison glands of *Scorpio* are probably homologous with a pair of large glands in *Thelyphonus* said to emit an offensive and volatile fluid, only here the limbs have degenerated and the glands open one on each side of the anus.

Of the above-mentioned glands the *Galeodidæ* possess only one pair, and that of a very simple character. They open just within the genital aperture and probably yield a sticky secretion for the eggs; there are no poison glands, no spinning glands, no "stink" glands. This is important, for it indicates that none of these glands in their specialised forms were present in the ancestral Arachnid. Indeed, this is obvious from the fact that they do not appear in exactly the same place and character in any two existing Arachnids, whereas had they developed in the ancestral form, we should have found more uniformity in their distribution and character in its descendants. But the *Galeodidæ*, if they have no glands, are as we have noticed above, extremely rich in bristles and hairs, and this same character we may safely predicate of the ancestral form. We shall probably then not be far wrong if we trace back all these glands to the small cuticular sacs out of

<sup>1</sup> It is worth noting that the marvellous web-spinning of the Spiders, and secondarily also the peculiar form of their abdomens are, in all probability, due to the early fixing of their spinning-glands far back on the abdomen. This position, the movement being from the waist, gave the threads a longer throw.



the bases of which in the primitive and more soft-skinned ancestor the bristles grew. The material which originally formed a bristle may be supposed to have been retained in a modified and fluid form within the sac which, in its turn, grew larger and larger to form the highly specialised poison or spinning glands of the modern Arachnids. I feel sure that an exhaustive comparative study of the bristles and glands of the Arachnida would completely establish this.

Let us then briefly sum up the characters which we can safely attribute to the ancestral Arachnid as soon as the evidence of the Galeodidæ is added to and compared with that obtainable from the other Arachnids.

We must picture to ourselves a loosely segmented hairy creature showing a slight waist-like constriction between the sixth and seventh segments. The first three segments are fused together and distorted in such a way as to range two pairs of limbs round an anterior mouth which is at the tip of a kind of beak. These limbs are specialised for seizing prey and crushing it in front of the mouth. The four following pairs of limbs are used for locomotion, while those of the segments behind the waist which are often swelled up by liquid food are more or less useless and degenerating. This, in brief, would represent the form from which, by modification and specialisation in various directions, all the existing Arachnida could be derived.

Having now reconstructed an ancestral form for the Arachnida, we ought with its help to be able to answer some of the questions relating to the probable affinities of the Arachnida to the Insecta and to the Crustacea. A few words on this subject will still further emphasise the utility of the analytical method here advocated and adopted.

It is now almost universally admitted that all the different Arthropods are to be deduced from Chætopod Annelids. A question still to be decided, however, is, are they distinct and separate modifications, or have they branched off from one another, starting from some original Arthropod which linked them all with the Annelid? Many have been the proposed lines of descent of the Arthropods from some

common Annelidan ancestor. The chief use for these genealogical trees has been to emphasise and drive home the doctrine of descent; they have too often been nine-tenths guess work, the available facts being quite insufficient to warrant such elaborate conclusions. Now it seems to the present writer obvious that the only possible means of establishing without dispute the relationships of animals derived from a segmented ancestor is to analyse carefully the arrangements and distortions of the segments characteristic of each group, ascertaining, as far as possible, the physiological significance of these arrangements and distortions. As above stated, we must analyse each fusion qualitatively as well as quantitatively. It will only then be possible to see whether and how far modifications of segmentation can be deduced from one another or are distinct and separate. If they can in any way be deduced from one another, we should then have some solid foundation for a genealogical tree, if they are distinct and separate, then each group must have arisen separately and have no relationship to any other group besides that involved in common origin from Chætopod Annelids. Few more striking illustrations of the necessity of discovering and comparing what the present writer has termed the "essential morphology" of the Arthropod groups could possibly be given than the recent controversy as to whether the Arachnids are not related to the King-crab and its fossil allies. The anatomical and morphological resemblances on which this affinity was based were really remarkable, although it is true they were met by an almost equal number of dissimilarities. These latter, however, could not disprove the argument based upon the striking likenesses. The difficulty, however, vanishes if we set ourselves the task of ascertaining whether the essential morphology of the King-crab has any resemblance with the essential morphology of the Arachnida. No one, I think, will dispute the accuracy of this argument even if they are not satisfied with the present writer's published attempts to elucidate the essential morphologies in question. The results arrived at are the following: The Crustacea, among



which the King-crab finds its place, appear also to have originated by the adoption on the part of a Chætopod Annelid of a peculiar method of feeding. This consisted in bending round the mouth with its large prostomium or upper lip ventrally so that the limbs arranged along the body could rake the food into the ventral middle line and push it into the mouth. In process of time, various groups of those limbs which were nearest the mouth became specialised, some into jaws chewing the food within the mouth aperture, others into sensory feelers (antennæ).<sup>1</sup> There seems to me no possibility of connecting this method of modifying the anterior segments, this ventral bend of the first segment of the Crustacea with the initial specialisation of the ancestral Arachnid which as above sketched involved a tilting upwards and backwards of the first segment and the fusion of the upper and under lips to form a rigid sucking beak. The two must be regarded as separate and distinct modifications of their Annelidan ancestors. I repeat that, without such a qualitative analysis of the segmentation as is here suggested, I do not see how the question as to whether *Limulus* was an Arachnid or not, a question that for more than a decade has divided zoologists into two almost hostile camps, could ever have been finally settled, as I believe it now to be.

The insects are another group of Arthropods with which it has been thought the Arachnids might be associated. Some remarkable resemblances occur here again as in the cases of *Scorpio* and *Limulus*. The Insecta, like the Spiders, typically have waists and ten segments behind the waist. The number of segments in front of the waist does not correspond, but it was thought that, if a pair of small anterior antennæ had disappeared from the Arachnids, then the only difficulty would be removed. It is true that the Arachnids had typically no trace of a “ head ” marked off by a “ neck,” but some approach to a head region could, it was thought, be found in the helmet-like plate of *Galeodes*,

<sup>1</sup> The arguments on which this is based can be found in the author's book on the *Apodidae*, *Nature Series*, 1892, and in two papers on the Trilobites in the *Q. Journ. Geol. Soc.*, vols. li., lii.

behind which came, as in the insects, a thoracic region with three pairs of limbs.

Here it will be seen that the whole stress is laid upon the quantitative differentiation of the segmentation; whereas as soon as the qualitative differentiation of the anterior segments of the two groups are compared it is seen at once that, in spite of all remarkable resemblances, the *Insecta* and the *Arachnida* have nothing in common except descent from a *Chætopod Annelid*.

The initial specialisation of the ancestral insect was undoubtedly also an adaptation to the method of feeding adopted. Unlike the *Arachnids*, the food was probably from the first supplied by the vegetable kingdom, and the limbs nearest to the mouth (except the first pair which became feelers) were specialised into biting jaws for tearing and crushing the edges of leaves or the surfaces of stalks. Highly developed locomotory powers were hardly needed for this method of feeding, so that an annelidan stage with only a head region showing the typical specialisation of the *Insecta* long persisted, and still persists, in the grub or caterpillar stages. We have no caterpillar or grub stage in the *Arachnids* because, being from the first carnivorous, the necessity of catching their prey required the development of highly specialised locomotory powers concurrently with the adoption and perfection of their method of feeding.

In this case again, then, the analytical method is emphatic against there having been any close affinity between the *Arachnida* and the *Insecta*. The three chief groups of the *Arthropoda*, the *Insecta*, the *Crustacea* and the *Arachnida* must be regarded as separate and distinct derivatives of the *Chætopod Annelids*.

I should like to add in conclusion that in thus insisting upon the necessity of solving the questions of affinity between the *Arthropods* by appeal to their "essential morphologies," by which I mean the peculiar structural modifications of their segments treated as physiological adaptations, I am aware that the method is not a new one; it lay in the direct path of morphological research. It needs emphasising, however, because the hopes which the study



of embryology held out to us of solving such questions by short cuts, hopes which have not been and, I fear, never will be realised, have drawn away attention too much from the analysis of adult forms. Every animal group contains in itself the record of its past, if we could decipher it. In some cases, such as those here dealt with, this is comparatively easy, but in others the record is so obscured that we may have to wait for fresh clues before we can unravel it.

In the meantime a more thorough comparative analysis of the forms of life at our disposal would not only bring us nearer to the solution of many an interesting problem, but would actually reveal to us clues which lie around us waiting to be recognised.

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## THE CELL-MEMBRANE.

### I.

THE membrane by which the cells of vegetable tissues are bounded has generally been described by most authors as originating in a fairly uniform condition, and consisting at first at any rate of an almost or quite homogeneous sheet of cellulose. After its first formation it increases in surface and later in thickness, its composition remaining unchanged. Finally, in most cases it undergoes chemical transformations in its substance, becoming suberised, cutinised, lignified or mucilaginous. As generally described, therefore, cellulose alone must be regarded as the basis of the cell membrane and the modifications met with are due to changes in the cellulose, leading to the formation of other bodies, which are then found mixed with, and largely replacing, the latter.

The study of the cell-wall may thus be carried on under the two heads of the primitive membrane and such modifications of it as do not present the latter changes, and the modified membranes which are characteristic of woody, corky and mucilaginous cells.

In dealing with the former of these, what indeed may for purposes of discrimination be called "unchanged" cell-wall, it is well to recall the theories of its composition which have been advanced in recent years. Without entering into much detail we may mention the two hypotheses of Naegeli and Strasburger. According to the former the molecules of cellulose are aggregated together into quasi-crystalline groups, the micellæ, which are separated from each other by delicate films of water. According to Strasburger, the theory of the micellar aggregations is unnecessary and the structure is regarded as having a network arrangement, the meshes of the network containing water.

A later theory, advanced by Wiesner (1), has however much to recommend it, especially in the light of recent researches made upon the structure and chemical composition



of the wall. On this hypothesis the membrane is composed of a number of minute more or less rounded protoplasmic bodies, the dermatosomes, which so long as the cell-wall is immature and capable of growth are united together by delicate filaments, also composed of living matter. The cellulose is formed by these dermatosomes, which become embedded in it. New dermatosomes are continually constructed from the substance of the threads, so that the wall grows by a process of intercalation somewhat recalling Naegeli's intussusception. Successive layers of the membrane, however, may be formed so that the thickening of the adult wall may be due to apposition, while each layer is formed and increased by intercalation of dermatosomes.

The membrane which bounds two contiguous cells can more or less easily, as we shall see, be separated into two layers, often by merely mechanical methods, more frequently by chemical ones. Wiesner hence infers that the threads which connect the dermatosomes of two contiguous layers can be more easily ruptured than those which exist in the substance of the several layers of the wall.

The great value of this hypothesis will appear later. For the present we may note that according to it the whole substance of the membrane is in contact with protoplasm and not merely its internal surface. We have therefore the possibility of an active chemical change of the substance of the wall and not the probability of merely a decomposition of inert compounds, commonly described as a process of degradation.

The generally received idea of the cell-membrane is thus that of a homogeneous sheet of cellulose, formed in some way by a kind of secretion from the protoplasm, and only showing differentiation of its substance when it undergoes such a change as that of lignification or one of the others spoken of. In a tissue which has much-thickened walls, it is not difficult to recognise a middle layer lying between the cells in the substance of the wall, and to notice that the tissue can be disintegrated into its constituent cells by the process of solution of this layer. This *middle lamella*,

as it is usually called, is thus easily proved to be of different chemical composition from the remainder of the tissue.

Passing over for the present the question of the exact composition of this middle lamella in the much-modified cells of wood, sclerenchyma, etc., and turning to the young tissues, consisting of so-called unchanged cellulose and situated in the meristem of the apex of the axis, it is somewhat interesting to find that from their very commencement we can find evidence that the membrane is not homogeneous, but that whatever be its original substance something of the nature of a middle lamella can always be proved to exist. By appropriate solvents or treatment that will be described later, the thickness of the cell-membrane can be split into two and the young as well as the adult cells set free from each other, each retaining a complete cell-wall.

Besides this evidence of a material differing from cellulose forming part of the cell-wall from its early condition, we may note the presence in the intercellular spaces between the cells of parenchyma of a substance which Russow (2) and others described as "intercellular protoplasm," and which sometimes appears as a delicate lining to the space and sometimes takes the form of concretions of various shape and bulk, occasionally filling the intercellular passage. The true nature of this so-called intercellular protoplasm was by several botanists, notably Gardiner (3), determined to be much more allied to the substance of the cell-wall than to the protoplasm, though it does not give the micro-chemical reactions of cellulose.

The idea of the homogeneous nature of the cell-wall is thus seen to be at variance with the facts. It is strange that it should have been put forward so definitely up to quite recent years, as the study of the works of the botanists of forty to fifty years ago shows that there was then considerable discussion upon the subject.

As early as 1825, Braconnot (4) extracted from the roots of several plants, especially those of the turnip and carrot, from the bulbs of the onion, and from the stems and leaves of many herbaceous plants and trees, a certain feebly acid substance to which he gave the name of pectic acid. He



found it had a very wide distribution, not only in the vegetable kingdom, but in the substance of the individual plant. About the same time, or a little earlier, Payen (5) extracted from the root of *Ailanthus glandulosa* a peculiar vegetable jelly, which was closely related to, if not identical with, Braconnot's pectic acid.

These discoveries attracted the attention of various chemists and botanists to the subject, and during the next few years much was ascertained about pectic acid and its reactions. Vauquelin (6) in 1829 published an account of some methods of preparing it, and of a study of its properties.

During the next ten years, the work of Mulder (7) and Fremy (8) added to our information as to the chemical peculiarities of this body, and it soon appeared that it did not exist alone, but that at least one other body, *pectine*, was present also. Fremy later called attention to a third similar compound to which he did not at first give a name. He describes it as existing in fruits in the condition of a pulp, and being under the action of an acid rapidly converted into pectine. He distinguishes it carefully from cellulose, but says he is not able to separate the two, and hazards the opinion that it may be only pectine combined with a certain amount of lime. Later Fremy gave it the name of *pectose*.

The existence of bodies of this character in bulky tissues, and the possibility of their extraction by various solvents having been demonstrated, attention was directed to their whereabouts and their relationship to other elements of the tissues. They were soon associated with the cell-membranes, Mulder suggesting that though the form in which they exist in different parts of the plant is not known, it is probable that they are to be found in the thickening layers or depositions in the cell-wall. They can be extracted by alkalies from the cell-partitions.

Payen (9) in 1846 added another contribution to our knowledge by pointing out that in certain plants these pectic bodies exist in combination with the metals of the alkalies and alkaline earths, chiefly potassium and calcium. He located these compounds chiefly in the epidermal tissues,

the walls of the cells of which consist in large part of them. He held that the mineral salts were intercalated with other substances in the body of the cell-wall.

In a latter paper of Fremy's (10) written in 1848, he gives some account of his researches on the localisation of the bodies, which in his earlier work he had only indicated as existing in plant tissues. The hitherto unnamed substance he calls *pectose*, and declares it to be a constituent of the membrane so closely connected with the cellulose, and so easily changed by various reagents, that he had found it impossible to separate the two. Like cellulose it is insoluble in water. Fremy found it in the cell-walls of green fruits, such as the apple; in those of the roots of many plants especially such as are succulent, like the carrot and turnip; also in the fibres of the cortex of the axis. The pectine of other authors he considers to be a derivative of pectose.

Mulder extended the localisation of pectose to the collenchyma, and the thin-walled parenchyma of *Opuntia Brasiliensis*, and says that it occurs also in the external parts of the thickened walls of the laticiferous vessels or cells of *Euphorbia Caput-Medusæ*. Referring to Payen's researches he suggests that the pectic acid and calcic pectate of the latter are derivatives of pectose. Harting (11) suggests that the thickening matter of collenchyma, bast fibres and many other thickened parenchymatous cells, as well as the substance of most thin-walled cells consists of pectates or of pectose, which he supposes to be isomeric with pectic acid. Both these writers point out that while cellulose gives a blue colour in treatment with iodine and sulphuric acid pectose remains uncoloured under the same conditions.

These views, however, did not remain unchallenged. Other writers, among whom may be mentioned Poumarède and Figuier, denied the existence of pectic acid and considered that the wall is essentially homogeneous at first if not always, and that pectose and cellulose are essentially identical.

The substance forming the middle lamella being most easily recognisable and the latter layer being in so many



cases easily visible, the view arose that it consists of a sort of intercellular substance, or cement, joining contiguous cells together. This was advanced by von Mohl and supported by Mulder and Harting. These authors speak of its being very variable in composition and consisting very largely of pectose, filling the spaces between the cell-walls and penetrating into the inner layers. They also held that it forms the mass of the little projections or concretions which often extend into the intercellular passages. The layers internal to the middle lamella they regarded as chiefly cellulose.

Harting's conclusions on the formation and growth of the cell-wall are that the primary cell-wall forms the internal layer and that it becomes thickened by a process of intussusception from within outwards, the primary membrane being cellulose, while pectose is developed in the external region as the wall thickens. Von Mohl on the other hand holds that the intercellular substance as well as the pectose is not formed in the wall, but infiltrates into the cellulose, masking the reactions of the latter.

None of these writers agreed with Payen, that the so-called intercellular substance was composed of alkaline pectates. In a later paper, Payen (12) points out a difference that can be established in this substance in different places. He found he could disintegrate the tissues and separate the cells by treating pieces of the former by the successive action of dilute acids and alkalies. When so treated the lateral or radial walls could be easily dissolved, but not the tangential ones, so that the cells separated in radial chains. Hence he suggests that the lateral walls were separated by pectates and the others by laminæ of cellulose.

A method of distinguishing between cellulose and the various pectic bodies was pointed out by Fremy (13). This consisted in treating the tissue with ammonio-cupric sulphate (Schweizer's reagent). This reagent dissolves pure cellulose, while the group of pectic bodies remains apparently unaffected, though really much modified, insoluble cupric pectate being formed. Alkalies on the other hand do not affect cellulose, but dissolve the pectose by converting it into soluble pectates. He agrees with the other writers

that the pectose is situated under the internal layer of cellulose.

Kabsch (14) found that when a cell-membrane is swollen by the action of chlor-zinc-iod, the inner layers only take on the blue coloration of cellulose and that the middle lamella, or so-called intercellular substance, varies in different cases, sometimes remaining colourless, sometimes appearing yellow and occasionally taking a pale blue tinge. He consequently locates the pectic bodies in the middle layer and says that the inner layers consist only of cellulose. The middle lamella thickens as the cells grow older and the increase of the pectic material is due according to him to transformation of the substance of the primary membrane.

Vogl (15), who wrote at about the same time as Kabsch, takes the same view as to the origin of the pectic substances in the wall. His experiments were made chiefly on the roots of *Taraxacum officinale* and a species of *Podospermum*. He found that the innermost part or layer of the cell-membrane is composed of cellulose, next to which is found a layer of a mixture of cellulose and pectose, and concluded that the latter was derived from a process of transformation of the older part of the cell-wall. Most externally he identified the so-called intercellular substance, and he says he considers it due to a transformation of the cell-membrane proceeding from without inwards, the resulting material being pectose. Vogl accounts for the cell-fusions of the laticiferous vessels of those plants by a transformation of the original cellulose septa into a soluble pectose which becomes dissolved.

Wiesner (16) a year later, supporting the conclusions of Kabsch and Vogl, carries them further and applies them to the lignified and corky cells as well as the parenchyma. Working especially on the beet, he describes the fate of all the tissues, saying that all the cells alike begin by being the seat of pectic transformations from cellulose, and that while the cortical membranes remain in different stages of this metamorphosis this is in woody and suberised cells followed by further transformations, leading to the recognition of lignified and corky walls. There have thus been advanced



in the middle of the present century two opposite views of the composition of the wall or of the interpretation of the facts which have been observed.

A further controversy has been conducted with regard to the composition of the middle lamella or, as it was once called, the intercellular substance. The constant existence of this part of the membrane was first put forward by von Mohl (17) in 1835, and his views were much debated, Mayen opposing and Schleiden supporting them. Mulder and Harting, as mentioned above, distinguished pectose as forming at any rate part of this layer; Payen considered it formed of mineral pectates, principally those of calcium and potassium. Unger took up the position that its substance, differing from cellulose, was first formed in the tissue and that the cell-wall is a product of its transformation. Wigan (18) joins Mayen in denying its existence as a separate layer, and maintains that it is only a product of transformation due to chemical or physical modification of the oldest layers of the cell-membrane.

Schleiden on the other hand held it to be a true secretion of the cells which is caused to accumulate on the outside of the membrane. This, on the whole, is the view of Schacht, who says that like the cell-wall itself it is probably a product of the primordial utricle. Schacht writes very guardedly on the subject, suggesting that it is not certain that it increases in thickness as the cell-wall grows, but admitting that it seems thicker between adult cells than between young ones. Its reactions according to this author are that it is insoluble in concentrated sulphuric acid, soluble in alkalies, and destroyed by oxidising agents more rapidly than the cell-wall proper. Also, it is more capable than the latter of resisting putrefactive changes.

Unger's view of this substance being the antecedent of cellulose, is supported by Dippel in 1851 (19). This author describes it as consisting of a kind of jelly which persists as such for some time, cellulose being formed upon its surfaces. As development proceeds it becomes converted into cellulose, but even then it only turns brown and not blue on treatment with iodine and sulphuric acid, this difference of

behaviour being due to infiltrations of nitrogenous matters into it.

The intercellular substance was thus regarded by some of the older investigators as a primitive, jelly-like material, ultimately giving rise to cellulose, and by others as a product of secretion formed by the protoplasm and made to accumulate in the outer part of the membrane. By some its composition is not stated, especially by Schacht, which is rather surprising, as he carefully studied its reactions. As already mentioned, Mulder, Harting and Payen were agreed that pectic compounds entered into its structure. Dippel says it is not cellulose, but gives no opinion as to its nature.

In the writings of Naegeli, Sachs, and other later writers, the term "middle lamella" replaces "intercellular substance". It was proposed to call it the "primary membrane," but as this suggested a definite origin and was not exactly in line with the theory of growth by intussusception, which was then coming into favour, the term "middle lamella" came to be adopted. This certainly had in its favour the fact that it was essentially non-committal. The writers of this period leave its nature undetermined. Sanio (20) in 1873 speaks of it in *Pinus sylvestris* as "Zwischensubstanz" and describes it as a gelatinous material intercalated between the radial rows of the generating cells. Both Sanio and Dippel lean to the opinion that whatever its chemical nature it arises from decomposition of the original cell-wall, a view exactly opposite to that advanced by Unger some years previously.

When Wiesner put forward his hypothesis of the composition of the cell-wall he recognised the existence of this middle region and pointed out that very young cells could be separated easily by its severance; much more easily, indeed, than older ones, and concluded that the threads uniting the dermatosomes were much more easily ruptured in that region than in the other layers. The rupture could be caused in some cases by mere mechanical traction, in others by chemical reagents such as strong hydrochloric acid. Wiesner did not consider there was necessarily any chemical



difference, though he admitted it in certain cases, but even then he did not hold that it proceeded from any metamorphosis of the membrane which took place gradually at the periphery of the cell-walls.

The view that such chemical difference does exist and that the opinions of the earlier workers in this field are in the main accurate, receives some support from Van Tieghem's observations on the progress of putrefaction set up by bacteria. In his *Traité de Botanique* (21) he shows that *Bacillus Amylobacter* disintegrates vegetable tissues by dissolving the middle lamella. He says that the cellulose of the wall exists in two varieties, one of which is split up by the micro-organism into butyric acid, carbonic dioxide and hydrogen, while the other is unaffected. As Van Tieghem gives no reactions which are distinctive of these two varieties, it is clearly open to us to hold the view which accords with earlier investigations, namely, that the material dissolved by the bacterium is pectic in its nature and that pure cellulose is unaffected by it.

Besides the middle lamella, other modifications of the original wall need mention. Chief among these we have the so-called intercellular protoplasm of Russow (2). He described this substance as forming in certain cases a delicate membrane or lining-layer, coating the intercellular passages. This substance has been critically examined by Gardiner and by Schenck, both of whom deny its protoplasmic nature. Gardiner (3), relying on certain staining reagents, especially methylene blue, advanced the view that it is a product of cellulose decomposition, probably a kind of mucilage, and states that it varies very much in composition in different cases. Schenck held that it is of the same general nature as the middle lamella, but declined to give a more definite opinion as to its nature. Mangin considers it to be composed of a mixture of pectic bodies.

The rod-shaped filaments and concretions of various shapes which are found in the intercellular spaces of many of the Pteridophytes and in the integuments of the seeds of some of the Papilionaceæ have also been variously stated to be protoplasmic or to be formed of cutinised material.

There is great reason, however, to believe from Mangin's researches that these also are formed largely if not entirely of various pectic compounds.

The various investigations that have been summarised above, point unmistakably to the conclusion that the cell-wall is originally far from homogeneous, and that while cellulose enters very prominently into its composition there are present in it a number of other substances which have hitherto been somewhat loosely described under the names of pectose, pectine and compounds of pectic acid. The modifications of cell-wall which give rise to gums and mucilages, all of which are probably very complex, may well be derived from these and not from the cellulose constituent at all. At the same time it must not be overlooked that several modifications of so-called cellulose exist, differing from each other possibly in the degree of their hydration.

In considering the composition of cell-wall, as far as it has been determined at present, the researches of Mangin (22) on the subject are most complete and of the first importance. Till his memoir appeared the whole group of pectic compounds was ill-defined, and nothing very definite was known as to the distribution in plant cell-walls of most of them.

These compounds can now be arranged in two series, one of the latter comprising bodies of a neutral reaction, while those of the other are feeble acids. In each there are probably several members, which show among them every stage of physical condition between absolute insolubility and complete solubility in water, the intermediate bodies exhibiting gelatinous stages, characterised by the power of absorbing water in a greater or less degree.

Of the neutral series the two extremes are presented by *Pectose* and *Pectine*. The former is insoluble in water and closely associated with cellulose in the substance of the membranes; the latter is soluble in water and forms a jelly with more or less facility.

In the other series the two most noteworthy members are Pectic and Metapectic Acids. The former generally exists in the membranes in combination with the metals of



the alkaline earths, especially calcium; when in the free state it is insoluble in water. Metapectic acid is soluble in water without forming a jelly. The two series are closely related to each other, for by the action of heat, acids and alkalies the various members of both can be prepared from pectose. The final product of the action of the reagents is the freely soluble metapectic acid.

Mangin gives their distinctive reactions as under:—

*Pectose*.—The actual properties of this substance are not at all easy to ascertain, nor can they be said to be well known. The material is so closely associated with cellulose that it cannot be prepared pure at present. The reagents that separate it from cellulose convert it either into pectine or into pectic acid, the former being soluble in water, the latter in alkalies. The membrane can be shown to contain the two constituents by the action of Schweizer's reagent, which when used with the proper precautions dissolves out the cellulose and leaves the framework of the cell apparently unaltered; it then consists, however, not of pure pectose, but of a compound of pectic acid with the copper of the reagent.

*Pectine*.—This body swells up and dissolves in water, giving a viscid liquid which is very difficult to filter and which soon forms a jelly. This is the body which Fremy found in ripe fruits, and it exists in many mucilages. It gives no precipitate with neutral acetate of lead, but is thrown down by the basic acetate in the form of white flocks. If boiled for several hours in water it is converted into an isomer, *parapectine*, which is precipitated by the neutral acetate. Further boiling with dilute acids converts it into *metapectine* which is precipitated by barium chloride.

*Pectic acid*.—This body is insoluble in water, alcohol and acids; it forms soluble pectates with alkalies and insoluble ones with the metals of the alkaline earths, of which calcic pectate is most widely distributed. It dissolves in solutions of alkaline salts, such as the carbonates of sodium and potassium, stannates, alkaline phosphates, and most organic ammoniacal salts, forming with them double salts which gelatinise more or less freely with water. Its solutions in

alkaline carbonates are mucilaginous and difficult to filter, while when oxalate of ammonia is the solvent it is perfectly fluid and filters readily.

*Metapectic acid*.—This is a body with an acid reaction, freely soluble in water, and forming soluble salts with all bases, especially calcium and barium, which precipitate pectic acid. Metapectates warmed with an excess of alkali take a yellow colour. This body and its compounds approach the gums in their composition.

Metapectic acid can be prepared from either pectine or pectic acid by boiling with excess of alkali. Acted upon by sulphuric acid it splits up into a dextrorotatory crystallisable sugar, apparently identical with arabinose, and into a little-known organic acid, indicating by this behaviour some relationship to the group of the glucosides.

The reactions just given clearly show that these pectic bodies form a group quite distinct from the celluloses which are known. The ease with which they are altered by the reagents used for their extraction readily marks them off from the latter, as do the products of their oxidation. If warmed with nitric acid, instead of being oxidised to oxalic acid like the carbohydrates, they give rise to mucic acid. They are further all insoluble in Schweizer's reagent and they give no blue coloration with iodine in any combination.

In endeavouring to ascertain the various ways in which these bodies are associated with cellulose in the cell-membrane, Mangin relied partly upon staining reagents and partly upon the action of various solutions in which one or other of the constituents of the wall are soluble. His investigations do not take into account the modifications which lignified, suberised or mucilaginous walls present, but only those in which the membrane has been considered to consist of unchanged cellulose.

A marked difference between cellulose and pectic bodies soon comes out in studying the action of stains upon them. Cellulose acts as a feeble base and takes up, therefore, acid stains, particularly those containing nitrogen. Pectic compounds, on the other hand, act as acids and require basic stains.



Hæmatoxylin, methylene blue, vesuvian brown and quinolin blue stain the pectic constituents of the wall and not the cellulose as has hitherto been supposed. The composition of the wall in any case can be better ascertained, however, by the action of solvents. If sections be placed in freshly prepared Schweizer's solution and left for several days, the fluid being renewed daily, the cellulose becomes gradually dissolved, complete removal of it being effected in the soft tissues in about three to four days. The sections must then be washed several times with water and later with a solution of acetic acid, containing from three to five per cent. of the latter, till all trace of the copper has disappeared. The shapes of the cells can then be seen to be unaltered, although naturally the sections have become very fragile. That the cellulose has been completely extracted is shown by treating the tissue with iodine and phosphoric acid, when the walls become pale yellow instead of blue. If the sections have been rather thick the cellulose will have disappeared from the membrane, but as the solution of this substance in Schweizer's reagent is slightly viscid, it will not all have been removed from the sections by the washing with water, and the subsequent treatment with the dilute acetic acid will have precipitated it in little clots in the intercellular spaces or sometimes in the interior of the cells. These little masses will, after the treatment with the iodine and phosphoric acid, stand out as blue patches among the yellow membranes. If now the stains for which the pectic bodies have an affinity be applied to the sections, the membranes all take them up freely.

The pectic compound thus remaining after removal of the cellulose is not unchanged pectose, but has been converted in great part into pectic acid; for if the section be irrigated with ammoniac oxalate, in which this acid is soluble, all the membranes rapidly disappear. If instead of the oxalate the walls be dissolved in ammonia and then the latter be neutralised by dilute acetic acid, a gelatinous precipitate falls, which can be stained with a basic stain such as methylene blue.

Another method of demonstrating the mixed nature of

the wall consists in dissolving away the pectose and leaving the cellulose. Sections of the tissue may be boiled for half an hour with two per cent. solution of hydrochloric acid. After repeated washings in water, they should be again boiled for some time in two per cent. solution of the hydrate of potassium or sodium and again washed thoroughly. The tissue will then stain a deep blue with iodine and phosphoric acid, but not with basic stains.

There is only one substance which behaves like the pectic compounds with basic stains—the *gelose* of the Algæ. This can be distinguished from the former bodies by being soluble in hydrochloric acid diluted with an equal volume of water, but being insoluble in alkalies.

By means of these methods of procedure, Mangin has ascertained that in Phanerogams, Pteridophytes and Muscineæ hardly any soft tissue is devoid of pectic bodies in its cell-walls. These are found conspicuously present in parenchyma, collenchyma, bast and meristem tissues, pectic acid and pectose being the compounds generally occurring. Pectic acid, as Payen pointed out, usually exists in the tissues in combination with calcium as calcic pectate. Mangin demonstrated this fact by steeping the tissue, cut into small pieces, in dilute hydrochlorate acid, or preferably in a mixture of one part hydrochloric acid and three parts of alcohol. The pectate was decomposed, the calcium being converted into calcium chloride and the pectic acid liberated. This being insoluble was washed with water till all the hydrochloric acid was removed. It was then dissolved in a weak solution of potassic hydrate or carbonate and the solution filtered. On neutralising with a dilute acid the pectic acid was thrown down in gelatinous flocks. Mangin found, as Payen had done before, that the middle lamella, von Mohl's "intercellular substance," consists almost or quite entirely of calcic pectate, which serves as a kind of cementing medium, joining contiguous cells together. When by any reagent it is dissolved, the cells separate from each other.

The dissociation of the tissues by the process of dissolving the calcic pectate can be effected more gradually



by a prolonged soaking in cold alkaline solutions, or in Schweizer's reagent; by this treatment double pectates which are soluble and gelatinisable are formed.

The pectic body which exists in the thickness of the wall survives this dissociating treatment and is probably the pectose of Fremy. What are the relationships between it and the cellulose have not yet been determined, but there is a very intimate association between the two, and this probably a mechanical one, as they can be separated, but only by methods which materially alter if they do not destroy one or both. Mangin's mode of preparation of it has been already described.

The pectose and calcic pectate are thus found to be both present in soft delicate tissues, but in different proportions. In the young cells of meristems there is but little calcic pectate, while pectose is in larger proportion. It is not certain that in these cells it is mechanically combined with or embedded in a cellulose matrix; it may be united more closely with it, forming a compound comparable to a glucoside which splits up under the action of an acid, yielding cellulose and pectic acid.

In older cells, among which intercellular spaces or passages have appeared, the proportion of calcic pectate is more prominent, though even in the younger ones the limiting layer is composed of this substance. This outermost layer is quite free from cellulose. The calcic pectate often collects over the surfaces of the intercellular spaces, being, in fact, a continuation of the middle lamella of the wall which has split in the formation of the passage. It is easy to see also how the small plugs or concretions which are often found in such spaces may be formed of the same material.

Though these two bodies are the forms of pectic compounds which are most widespread, many intermediate modifications are met with which present their own peculiarities with respect to solubility, affinity for bases, etc. Thus the pectates which form the middle lamella are sometimes gelatinisable, swelling up in water. Such a variety is found between the cells of the lacunar parenchyma of *Calla*

*æthiopica*, in the peduncle of *Narcissus pseudo-Narcissus*, etc. In *Narcissus* it occurs in the intercellular spaces.

As the wall of the young cell increases in thickness the secondary laminæ show a certain difference in composition, pectoses being most abundant in the layers nearest to the middle lamella and cellulose most prominent in the newest layers nearest to the protoplasm of the cell.

The dissociation of the young tissues shows the interesting peculiarity indicated by Payen, the substance joining the cells not being the same throughout. If transverse sections be taken, the dissociation easily takes place in the radial direction but not so readily in the tangential one, so that radial rows of cells are separated from each other. If a longitudinal section of the growing apex of a stem or root be examined the lines of easiest cleavage can be seen to converge towards the initial cells of the apex, each group being wrapped round by a thin membrane.

We may now turn to the question of the composition of the primitive cell-wall. Is this originally homogeneous? If so, it may be regarded as being from the first formed of an intimate mixture of cellulose and pectose, forming a kind of *cellulose* approaching a glucoside in nature. On this hypothesis it becomes thickened with layers of the same nature, and the middle lamella is not at first present as a differentiated region. Soon by a kind of intussusception a deposit of calcic pectate is produced in the middle of the wall; or such a deposit may arise from a decomposition of the pectose under the influence of the acid sap and the infiltration of soluble calcic salts.

On the other hand the primitive wall may be from the first heterogeneous the first lamina being formed of calcic pectate, which becomes very speedily covered on its two faces by layers of the mixture of cellulose and pectose. On this hypothesis the middle lamella is universally present, and in fact constitutes the "primary membrane" of the writers immediately preceding Naegeli.

Whichever hypothesis may be adopted there is no doubt that in soft tissues at the moment when cell division ceases the wall can be shown to consist of a middle lamella of



insoluble pectates, containing no cellulose, and lined on each side by mixed layers of cellulose and pectose. From that point onwards it undergoes throughout its substance continuous transformations which modify the disposition of its constituent substances, the middle lamella becoming conspicuously increased in amount.

In this connection it is well to remember Wiesner's hypothesis of the dermatosomes in the wall, as it is evident that such transformations of material may well be brought about under the influence of such protoplasmic bodies in the interior of the membrane.

The mode of deposit of the projections or concretions of calcic pectate may perhaps aid us in forming a true conception of what takes place. These pectates gradually tend towards the outside of the membrane, passing possibly as soluble pectic acid in its substance, and being combined with the metallic base at the external surface or in the intercellular space. In the young growing cell, just behind the zone of cell division at the growing point there is the maximum of turgidity or osmotic pressure. It is quite conceivable that in a free cell this is sufficient to cause a stream of soluble bodies to pass across the substance of the cell membrane from within outwards. This indeed would lead to the extrusion of such soluble pectates, or pectic acid, which may be well formed from the pectose in the membrane by the action of the dilute acid of the cell-sap, into the space around the cell, or in a tissue, into any intercellular passage. But in the case where the cells are not free, but have their neighbours pressing upon them, as they have in the young part of the growing zone, any membrane will be subject to a pressure from each side, owing to the turgidity of the contiguous cells. In this case the stream of pectates would not pass out of the cell, but would tend to accumulate in the middle line between the two pressures, in the region that is where the middle lamella speedily becomes recognisable.

In connection with the formation of the calcic salt from the acid body, we may recall Fremy's observations on the ferment which he discovered in the root of the carrot.

This has the property of causing the soluble pectic bodies to gelatinise. Recently Bertrand and Mallevre (23) have again investigated the action of this ferment *pectase*, and have discovered that its action is not to cause the formation of pectic acid as Fremy supposed, but a pectate of calcium. By careful experiments they have shown that if Fremy's mode of preparation of pectine be followed, and then the pectine be carefully washed with a mixture of alcohol and hydrochloric acid till all traces of calcium are removed, a solution of such pectine will not clot on the addition of pectase which is also free from lime salts. If a small quantity of calcic chloride be now added, clotting takes place gradually, the length of time required being proportional to the quantity of the calcium salt used. The formation of calcic pectate which can thus be induced outside the plant by ordinary laboratory methods may well represent what goes on in the plant itself. It is well known that in the case of many of the unorganised ferments the enzyme carries out a process which can quite easily be effected by the protoplasm alone. If we have as Wiesner suggests a kind of framework of protoplasm throughout the whole of the unaltered cell-membrane, and we have slowly passing into or through the wall, under the influence of the internal osmotic pressure, a stream containing soluble pectates, and the usual mineral bodies of the cell sap, in which calcium salts must always be included, there seems no difficulty in explaining the deposition of calcic pectate in the form of a definite lamina where the pressures from two contiguous cells oppose each other.

Mangin in his paper rather holds to the other view, judging from experiments in rupturing the young cell-membranes, that there is first formed a layer of pectates, that indeed the first microsomata that are accumulated across the cell spindle have this composition.

The formation of intercellular spaces probably depends upon the behaviour of the calcic pectate. During the period of cell division the cells contain only protoplasm with a little water and there is little internal pressure. The cells are in close contact with each other and polyhedral or



cubical in shape. As the cells are left behind, and from the growing rather than the dividing zone, they become vacuolated and osmotic pressure gradually becomes considerable. When the growth of the cells in turn has ceased, the osmotic pressure causes the membrane to be in a state of tension, so that the limit of its extensibility is reached and its elasticity is equal to the stretching force inside. At this time the calcic pectate at the angles of the polyhedral cells becomes gelatinous and under the strain it gives way at the points where the gelatinisation is complete. The middle lamella in fact ruptures at the angles, while the other layers remain intact.

This mode of regarding the formation of intercellular passages enables us easily to understand how some of them become coated with a thin layer of pectates. Into some of them at the angles the gelatinised middle lamella can be seen to extrude, forming little plugs or projections. There may further be a continuation of the passage across the membrane of the soluble pectates, which, not now being balanced by a similar stream from an opposing cell, make their way to the exterior of the membrane and appear as a thin coating over the surface of the passage. Hence may also be formed the curious projections of pectates which have been found as already mentioned in the parenchyma of many *Pteridophytes* and other plants.

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J. REYNOLDS GREEN.



# THE COAGULATION OF THE BLOOD.

## THIRD PAPER.

HAMMARSTEN'S theory of the cause of blood-clotting was formulated over twenty years ago, and it has stood the severe test of time, before which so many physiological theories fall to the ground. It still continues to be the best working theory we have on the subject. Put briefly it runs as follows :—

In the living blood, a proteid of the globulin class called fibrinogen exists in solution. When the blood is shed, the fibrinogen molecule is split into two parts ; one part is a globulin which remains in solution, the other and more important part is the insoluble proteid called fibrin, which entangles the corpuscles and produces the clot. This decomposition of fibrinogen is accomplished by the fibrin-ferment which is one of the products of the disintegration of white corpuscles, blood-tablets and other protoplasmic structures that occurs when the blood leaves the vessels or comes into contact with foreign matter.

This theory replaced the older one of Alex. Schmidt who taught that fibrinogen and paraglobulin were both necessary for the formation of fibrin.

Since Hammarsten's theory was formulated investigators have not been idle, and in two papers published in this Journal,<sup>1</sup> I have given an account of the principal work that has been done in relation to the question. This work includes that of Wooldridge who introduced the important method of studying coagulation in the blood-vessels themselves, and in not being content with mere experiments *in vitro*. He showed that the "tissue-fibrinogens," substances obtainable from most of the cellular organs of the body, will, when injected into the circulation of a living animal, produce intravascular coagulation. These tissue-fibrinogens are nucleo-proteids, and fibrin-ferment belongs

<sup>1</sup> Vol. ii., p. 369 ; vol. iii., p. 127.

to the same class of substances.<sup>1</sup> The other principal new fact that has been discovered is the great importance of calcium salts in the process, though as to the exact way in which these salts exercise their influence there is considerable diversity of opinion.

My reason for once more returning to this subject is that within the last few months Hammarsten has broken the silence of twenty years, and once more attacked the problem. In the paper<sup>2</sup> he has published, one notes again the hand of the master; there is the same thoroughness and lucidity which were so evident in his older work, though it is interesting to note that experiments *in vitro* are still exclusively relied on to support his conclusions. The special subject with which he deals is the *rôle* played by calcium salts in the production of fibrin from fibrinogen, and his endeavour to settle the differences between rival theories is attended with considerable success. I propose to devote the remainder of this paper to a brief consideration of his experiments and their results.

Though Hammarsten himself, Green, Ringer and Sainsbury, Freund and others had noticed the accelerating action of salts of lime in promoting coagulation, it was not until Arthus discovered that coagulation can be prevented by decalcifying the blood by the addition of an alkaline oxalate, and Pekelharing had followed up this work with new experiments, that the calcium salts were recognised universally as a *sine quâ non* in the process of blood-clotting.

There are two possible stages in the process where the favouring action of calcium salts might come in; one of these is in the genesis of the fibrin-ferment, and the other is in the action of the fibrin-ferment in converting fibrinogen into fibrin. Arthus believes that there is a very close resemblance between the clotting of milk by rennet, and that of blood by fibrin-ferment. In the curdling of milk by rennet, the first action is the action of the ferment itself producing a

<sup>1</sup> For the identification of fibrin-ferment as a nucleo-proteid see Pekelharing *Centralb. f. Physiol.*, vol. ix., p. 102, 1895; Halliburton, *Journal of Physiol.*, vol. xviii., p. 314, 1895.

<sup>2</sup> *Zeitsch. f. Physiol. Chem.*, vol. xxii., p. 333, 1896.



change in the proteid called caseinogen ; the second stage is due to calcium salts, which precipitate the changed caseinogen, as the curd of casein. Fibrin is similarly believed to be a calcium compound of fibrinogen. On the other hand, Pekelharing showed that calcium salts have the additional action of assisting the formation of fibrin-ferment from its precursor or zymogen. The main outcome of Hammarsten's work is to show that this is the only part that the soluble calcium salts of the plasma play. They are undoubtedly essential for coagulation, but after fibrin-ferment has once been formed their presence is no longer necessary. Or to put it another way, and adopt a new nomenclature : in the living blood no *thrombin* or fibrin-ferment is present ; that substance exists in the form of a zymogen, which may be termed *pro-thrombin* ; calcium salts act by converting prothrombin into thrombin.

Any one who has ever tried to prevent coagulation in blood by adding a soluble oxalate to it immediately it is shed will know that they will often fail. This is because they are not quick enough. If the oxalate is mixed with the blood sufficiently rapidly, it will prevent the formation of thrombin ; but if there is the least delay, prothrombin will pass into the condition of thrombin, and no amount of oxalate subsequently added will prevent the thrombin or fibrin-ferment from converting fibrinogen into fibrin.

In the present research, Hammarsten prepared specimens of oxalated plasma, specimens of oxalated solution of fibrinogen, specimens of oxalated solution of fibrin-ferment, and specimens of oxalated serum, which is practically a solution of fibrin-ferment with numerous other things as well. On mixing together such solutions of fibrinogen with such solutions of fibrin-ferment he always obtained, and frequently rapidly obtained, a typical and abundant formation of fibrin.

In this connection it is important to notice that oxalated preparations of this kind are not in the strictest sense of the word, decalcified. They are only decalcified in what Hammarsten calls Arthus' sense of the word. That is, the oxalate added is unable to combine with and displace the calcium which is directly in union with proteid matter.

This was previously pointed out by Schäfer<sup>1</sup> in connection with this same question, and by Ringer<sup>2</sup> in connection with the contractility of the cardiac muscle. No reference is made by Hammarsten to these researches.

Other investigators who have tackled the question of calcium salts in their relationship to blood coagulation are Alex. Schmidt and Lilienfeld, and the points of difference between these workers and those previously mentioned are cleared up by Hammarsten in the following way:—

The view of Alex. Schmidt, that lime salts act qualitatively like other neutral salts such as sodium chloride in promoting coagulation, though in the quantitative sense they are admittedly more powerful, is incorrect. Arthus is unquestionably right when he ascribes to calcium salts a definite and specific action. The action of soluble oxalates is also definite and specific, for by precipitating the calcium salts it neutralises this specific action, and thus inhibits the coagulation of the blood. Here again Arthus is right, and Schmidt who supposes that alkaline oxalates act in the same manner as excess of other salts of the alkalis in preventing coagulation, is wrong. Arthus, however, goes wrong in the specific action he attributes to the calcium salts. They are not necessary for the change of fibrinogen into fibrin. If a sufficient quantity of fibrin-ferment is present, fibrin-formation goes on as typically and abundantly in solutions which do not contain soluble lime salts (these having been removed by oxalating), as in those which do contain such salts. In this way the analogy drawn by Arthus between fibrinogen and fibrin on the one hand, and caseinogen and casein on the other breaks down. The specific and only action of the lime salts is that discovered by Pekelharing, in producing the genesis of thrombin or fibrin-ferment, from its precursor, prothrombin. Pekelharing's experiment that the blood-plasma contains a material

<sup>1</sup> In a preliminary note to the Physiological Society ("Proc. Physiol. Soc.," p. 18, 1895, in *Journal of Physiology*, vol. xvii.) Schäfer arrived at much the same conclusions regarding this point, and regarding Lilienfeld's thrombosin to be immediately alluded to, that Hammarsten presents more elaborately in his present contribution to the subject.

<sup>2</sup> *Practitioner*, vol. xxiv., p. 81.



(nucleo-proteid in nature, prothrombin by name) which is not fibrin-ferment, but which by the action of soluble lime salts becomes converted into another substance (also essentially nucleo-proteid in nature, but thrombin by name) is easily confirmed. This second substance is a powerful accelerator of the coagulation process, and is in fact fibrin-ferment.

Lilienfeld's facts and theories are wrong throughout. This worker stated that if he took a solution of fibrinogen, and added to it some acetic acid, he obtained a precipitate of a new material which he called thrombosin; if he then added calcium salts to a solution of thrombosin he obtained a formation of fibrin. Thrombosin may also be precipitated from a fibrinogen solution by nucleic acid, and this is what he considered to occur in actual coagulation; the nucleic acid of the nucleo-proteid in the blood first separates thrombosin from fibrinogen, and then the thrombosin is precipitated as fibrin by calcium.

It has already been stated that Schäfer could not confirm this, and no more can Hammarsten. The so-called thrombosin is no new substance, it is simply fibrinogen which is partially precipitable by the acids just mentioned. When it is dissolved in saline solution and a soluble calcium salt added there is neither coagulation nor precipitation if fibrin-ferment is absent, though if fibrin-ferment is present, even though soluble lime salts are absent, fibrin is formed in the usual way.

It may be added that Lilienfeld is equally wrong when he distinguishes between nucleo-proteid and fibrin-ferment. Fibrin-ferment is not a globulin; it is a nucleo-proteid. It is not the result of fibrin formation as Lilienfeld states, but all the facts at present at our disposal point to it as the main cause of the transformation of fibrinogen into fibrin.

Underlying the theories of Arthus, Pekelharing and Lilienfeld there is one fallacy common to all. All look upon fibrin as a calcium compound of fibrinogen or of some derivative of fibrinogen. Hammarsten states this is not the case. Both fibrin and fibrinogen contain calcium, but there is the same amount of that element in each.

W. D. HALLIBURTON.

## ON THE RELATION BETWEEN THE FORM AND THE METABOLISM OF THE CELL.

THE problem to which I wish to draw the attention of biologists in the following paper is one which, no doubt, has already excited a certain amount of interest, but which has not yet, as far as I know, been made the subject of special research. I allude to the question as to the relationship which may exist between the form and the metabolism of the cell. This subject is of peculiar importance at the present time, when morphologists are busy discussing the special mechanical factors of organic formation; its consideration is therefore likely to lead to wider views on the whole subject of development or rather of form-evolution than are usually entertained.

The problem of the organic formation of the body is not purely morphological; it has also a physiological aspect, inasmuch as the full play of the vital processes of an organism is the one necessary condition of its proper and complete development. The ontogenetic evolution of the body and its vital processes are thus inseparably connected, and it is impossible to understand its mechanical structure unless its physiology be also taken into account. I am inclined to emphasise this point, as it seems to me that too great prominence is now often given to the morphological aspect of the question, whereas metabolism, the fundamental process on which all vital phenomena are based, is almost overlooked as a factor in the problem.

Now it has long been recognised as a physiological fact that all the vital phenomena of an organism are only different expressions of its metabolism; consequently all the form-changes of an organism, being among its vital processes, must, in the long run, be the outcome of its own characteristic metabolism.

The remarkable fact that this evident truth has been so little taken into consideration can only be accounted for by the difficulty of combining the two groups of pheno-



mena—metabolism and organic formation. For example, metabolism is practically inconceivable without a fluid condition of the substance undergoing change, while, on the other hand, the idea of a definite form involuntarily suggests a fixed position of the particles of matter of which the organism is composed. This difficulty, however, is merely superficial, and vanishes as soon as we examine the two seemingly irreconcilable facts. A fluid stratum is certainly a requisite of metabolism. In the words of the ancient alchemists, *corpora non agunt nisi humida*. Only gases or dissolved matter can enter into the chemical relations required in the metabolism of an organism.

This truth ought not to be ignored, as it has been by those who have maintained that the cell substance is more or less compact and solid. Many have regarded the protoplasm of a cell, including its nucleus, as a sponge-like network, others, merely recently, as a thread-like structure, composed of numberless fibres. To Berthold and Bütschli, however, belongs the credit of strongly insisting upon the fluid nature of protoplasm. Those who hold the opposite view base it solely on the examination of dead and preserved objects; it is difficult to imagine how any one can maintain it who has studied the life processes in living cells, *e.g.*, the protoplasmic movement in a creeping Amoeba, the many-branched system of currents in a Myxomycete plasmodium, or the rotation of the protoplasm in a plant cell. On the other hand, there can be no doubt that protoplasm, although essentially a fluid, does contain some more solid and firm elements, *i.e.*, it is a compound of substances of various consistencies.

When we find ourselves face to face with the question, "What are we to consider as actually living in living matter?" we have but one criterion to assist us to a decision, and that is metabolism. Only where there is metabolism is there life. This is the A B C of physiology. Hence, we can only call those particles alive which are undergoing chemical changes. We must consider as not alive, in the most restricted sense of the word, all matter which is not at the moment chemically active, even though,

like reserve material, it may be drawn, when required, into the metabolism. For instance the starch granule in the plant cell, the glycogen particle in the animal cell, so long as they remain without chemical change, as reserve material in the protoplasm, are not living. They only become living substances when, decomposed and dissolved, they take part in metabolism. The inner and outer skeletal portions of the cell, and also certain solid intercellular substances such as bone and cartilage cannot be considered as living, in the real sense of the word.

There can, however, be little doubt that, in many cells, certain parts are in a state of active metabolism in spite of possessing a form so unvarying that it gives the characteristic stamp to the whole cell. Striped and smooth muscle fibre, the ciliated epithelial cell, and the infusorian cell are well-known examples of this. The question then arises: "How is it possible that a fluid mass such as, for instance, a ciliated cell, can have an unvarying and complicated form?" The more or less rigid connection of the particles which we necessarily associate with solidity cannot be admitted since that would make metabolism impossible. In attempting to solve this question, some have assumed that, in cells which possess an unvarying form, the protoplasm is of a medium consistence, half fluid, half solid, and there is little to be said against this suggestion. The degree of fluidity, *i.e.*, of mobility of the particles, varies greatly in different fluids, and it is therefore possible that, in some cases, living matter has the characteristics of a very thick fluid. On the other hand, a high degree of mobility of the particles is a *sine qua non* for active metabolism, which not only extends over the surface but penetrates the cell in its entirety. The presence of metabolism in such comparatively rigid forms as a muscle fibril or a ciliated cell implies great activity of the particles, and thus the assumption just mentioned, *viz.*, that of a semi-solid, semi-fluid consistency on the part of the protoplasm is of no real assistance in an attempt to reconcile the apparently contradictory facts of the active movement of the component particles and unvarying form.

In this case as well as in that of many other physio-



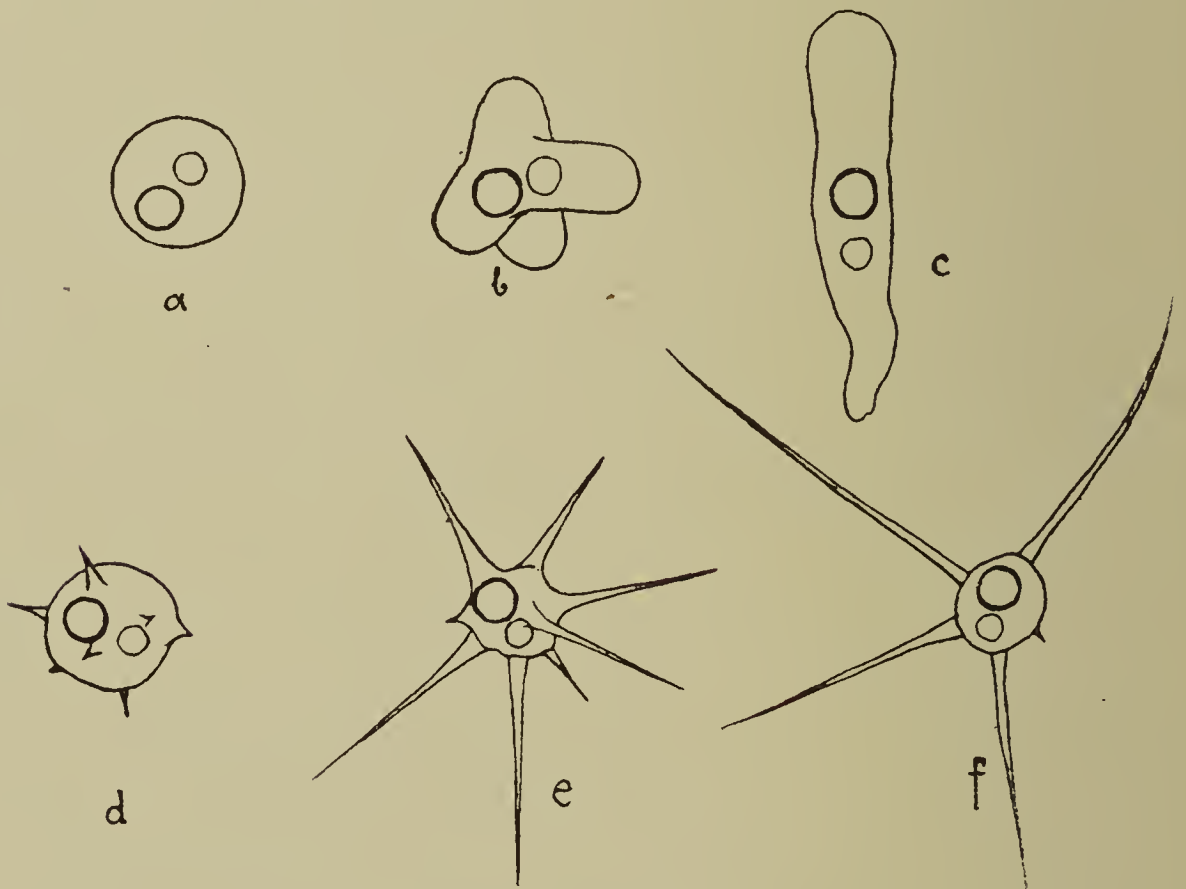
logical problems it is advisable first of all to study the primitive conditions exhibited by the lower cells, such, for instance, as are revealed to us by masses of naked protoplasm, *e.g.*, by the Amoeba. Such cells, in spite of, or rather just because of, their varying form appear to me to be capable of explaining not a few of the elementary problems of the organic formation of the body.

The organic form of the Amoeba is controlled by two principal factors, one physical and the other chemical. Physically, the Amoeba cell possesses the qualities of a fluid. This drop of fluid, however, is constantly exchanging its matter with the surrounding medium. As a fluid, the body of the Amoeba is subject to the physical laws which govern fluids and, if considered as existing solely under the influence of these laws, could well be supposed to assume a definite fixed form, let us say that of a sphere. This form the body of the Amoeba would permanently retain if the conditions remained unaltered. Change, however, will take place as soon as it enters into chemical relations with the surrounding medium. In these chemical relations, in other words in metabolism, then, we have the cause of the movement, of the flowing onwards and of the changes of shape of the Amoeba.

It is worth while to look a little more closely into the relations between the metabolism of the Amoeba and its change of shape. Let us take first, by way of example, the relation between respiration and the change of form. In connection with a previous observation by Kühne, I have elsewhere shown that a constant connection exists between the extension of the pseudopodia of the Amoeba and the amount of oxygen in the medium. With the withdrawal of oxygen the formation of pseudopodia and consequently the change of shape ceases; on the return of oxygen it recommences. This fact appeared to me to be of such fundamental importance that I repeated Kühne's experiments on large Rhizopods from the Red Sea, these being in many respects specially suited for the purpose. My results agreed entirely with those obtained by Kühne. The expansion of the long, straight, thread-like pseudopodia, such as the long rays which stream outwards from the cell of the Orbitolites,

ceased with the withdrawal of oxygen. The protoplasmic movements were arrested and the Rhizopod remained motionless until a fresh supply of oxygen caused the pseudopodia once more to expand. The formation of pseudopodia, and consequently the change of shape of the body, is thus evidently in the highest degree dependent on the supply of oxygen. On the other hand, total retraction of the pseudopodia can be caused by the introduction of certain acids, alkalies, or salts, into the medium surrounding the body. Sulphuric acid, potassium hydrate, or potassium sulphate, of a certain degree of concentration, added to the water containing an *Amoeba* at once cause retraction of the pseudopodia.

The dependence of the form of the organism upon its chemical relations with the surrounding medium is also clearly shown by the following facts, which a series of experiments have recently enabled me to demonstrate. *Amoebæ*, as is well known, are usually divided into different species



DIFFERENT FORMS OF THE SAME SPECIES OF AMOEBA.

a.—Spherical, during strong excitation.

b.—Beginning to move in the form of *Amoeba proteus*.

c.—Usual form of *Amoeba limax*.

d.—Beginning to assume the form of *Amoeba radiosa* after addition to the water of Potassium hydrate.

e,f.—Form of *Amoeba radiosa* under the influence of potassium hydrate.

according to the form of their pseudopodia. The *Amoeba proteus* is distinguished by broad finger-shaped pseudo-



podia; the *Amoeba radiosa* resembles a ball with numbers of thorn-shaped pseudopodia; the *Amoeba limax* consists, as it were, of one long club-shaped pseudopod which flows almost entirely in the direction of its longitudinal axis. It is an interesting fact that one and the same Amoeba may for a certain period be an *Amoeba limax*, then for another period an *Amoeba radiosa*, *i.e.*, it may assume two entirely different outward forms according to the condition of the surrounding medium.

A large number of small and very active Amoeba of the *limax* species (*c.*) were placed in a culture glass in neutral water. When, by a small addition of potassium hydrate, I rendered the water slightly alkaline, all the Amoeba, after the lapse of a quarter of an hour, assumed the typical form of the *A. radiosa* (*e, f.*) and retained this shape without showing the least interruption of their vitality.

Again, an *Amoeba proteus* having finger-shaped pseudopodia spreading in all directions, may be made to assume the form of an *A. limax*. If a chemical which causes the expansion of the pseudopodia be added so as to act only on one side, or if it be attracted by oxygen or food in one definite direction, the shape of the animal changes, *i.e.*, it assumes the form of one large pseudopodium extended towards the point from which the new influence emanates. The whole mass of the organism flows along this one pseudopodium, creeping towards the oxygen or food in the shape of a thick club, this shape being retained as long as its metabolism is influenced from the side. In spite of this rigidity of the form the whole substance of the body is in active movement; a current flows, as in a fountain, forwards in the longitudinal axis and backwards at the circumference.

These observations show plainly that, in a protoplasmic body which varies in shape, the form is determined by the different conditions and changes of the metabolism, and that every modification in the latter is associated with some definite shape. If a certain condition of the metabolism continues for a length of time, the form of body appertaining to it will also continue, even though, as in the case of

the Amoeba just described, the substance of the body may be in constant movement.

The Amoeba seen creeping in the form of an extended club towards the source of nourishment affords an answer to the question of how it is possible to have permanent shape of the organism where there is active movement of its particles. Given unchanging outward conditions, the form depends wholly on the unchanging character and direction of the metabolism. In a fountain or a gas jet, although the particles are in constant movement, not one of them retaining the same position for a moment, the entire jet retains its characteristic form as long as it is subject to the same conditions. The same is the case with living matter. A cell, in spite of its active metabolism, appears to us to be in repose. It gives us the impression of immovability, just as a gas or water jet conveys that impression although each particle is in rapid and incessant movement.

This view of the relation between metabolism and form gains an additional interest when applied to the phenomena of development. It is evident that if the metabolism of a cell is continually changing, the changes will find expression in the form of the organism, so long as this is not prevented by factors operating outside the organism. In this way, development is brought about. We know that the metabolism of the egg cell is from the first continually changing. The supplies of reserve nourishment are consumed and other matter appears in the cell and in its descendants. Here we have a marked example of the close connection between metabolism and change of form.

In this connection I would protest against the very wide-spread opinion that the egg cell, especially in the higher animals, must have a highly complicated molecular structure, much more complicated than that of any other cell. This appears to me to be an absolutely groundless assumption, recalling the so-called "Einschachtelung Theorie". Because a highly complicated organism develops from the microscopical egg cell, it is thought that the molecular structure of the latter must be highly complicated. I do not doubt that it is complicated, but I deny the assumption



that it is more complicated than the molecular structure of any other cell. We have only to imagine that the metabolism in the egg cell is continually changing, never remaining the same for two consecutive moments, so that each condition causes the following condition and is itself the outcome of the condition last preceding it. Considering how close is the connection between metabolism and change of form, each change in the metabolic exigencies of the developing organism must be responded to by a further and more complicated structural change. The assumption of greater complication of the molecular structure of the original egg cell is thus entirely superfluous.

It may appear as if the idea of molecular structure of living substance is inconsistent with that of the continual flow of matter. We have here, however, on a small scale, the same relation as that existing between change of form in the organism, and metabolism. Metabolism consists in chemical processes. These processes, however, are only brought about because each atom or group of atoms or molecules attracts, by chemical affinity, other atoms, group of atoms or molecules in a certain direction. This causes a continual flow of matter, some atoms or groups of atoms being withdrawn and others taking their places. If these atoms and groups of atoms are always of the same kind, and if their entrance and exit always take place in the same manner and direction, as must be the case so long as the metabolism of the whole remains unaltered, a certain ordering of the particles results which we must call structure although the whole substance is in motion, in a continual flow. It is only in this way that, for instance, the phenomena of the regeneration of the cell can be explained. A cell from which a portion has been removed can regain its original form provided that it is capable of producing the reserve matter required for its reconstruction. The reserve matter will reach the injured part through the usual channels, being attracted thither by the remaining particles, etc. Should the injured cell no longer have the power to produce the necessary matter for regeneration, *i.e.*, if the entire metabolism has suffered lasting injury, the recon-

struction of the lost part is impossible. If an Infusorian cell, for example, of a very characteristic and complicated form is cut in such a manner that only the one half retains the nucleus, all the cell particles requisite to life are to be found in this half, and these, through metabolism, will soon reproduce the original shape of the cell. The metabolism of the other half, on the contrary, having been permanently injured, it will slowly die, being incapable of regeneration. This important fact has been proved by a great number of experiments made by Nussbaum, Grüber, Balbiani, and others.

We thus find metabolism to exist in the closest causal relation with the production and preservation of form, and in all investigations and experiments on the mechanism of form-evolution it must not be lost sight of as constituting an important factor.

MAX VERWORN.





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## THE NATURAL HISTORY OF THE SEA.

THE study of the sea and its inhabitants owes much of its extraordinary fascination to the fact that all our gains in knowledge are the outcome of methods of groping for the truth by the aid of instruments hid from sight for the most part, and resembling in their operation the ventures of the gambler. The voyager who, on a clear night, surveys the heavens and the deep sea beholds two regions of research in which natural knowledge is increased in very diverse ways. The marvellous certainty with which the astronomer can foretell the movements and even the existences of heavenly bodies, stands in sharp contrast with the element of chance which enters into the pursuits of the student of life in the deep sea. The naturalist is content to dip into this great lucky-bag with the pleased expectation that he will be rewarded. His methods of capture, primitive in their simplicity, or crude in their complication, are themselves in contrast with the perfected instruments and methods of examination brought to bear on the spoils of his victory over this intractable element.

The great sea-captains and explorers from the earliest times were geographers in search of fresh lands who used the sea as a means of transport, and all the tradition of mystery which grew up in their minds, and is still part of every seaman's nature, survives and tinges even the scientific work of examining the physical and biological conditions of the ocean. It is still the unexpected that happens to the

naturalist or the physicist who goes down to the sea in ships. This is owing to the fact that the study of the sea, and especially of the animals and plants in it, is yet in its youth, and the progress of our knowledge is not to be measured by the milestones of volumes recording the work and speculation of recent years.

The two magnificent volumes which close the record of the work of the *Challenger* Expedition (1) are in every way worthy of their fellows in the series of fifty containing the whole account of this celebrated voyage. It is just a quarter of a century since H.M.S. *Challenger* sailed on a voyage which was to make discoveries, comparable only with those of Columbus and his immediate successors. The ocean which covers three-fifths of our globe was barely known to us, though admirable research had been steadily increasing our knowledge and speculations for a century. As an introduction to the two volumes containing the "Summary of Results," Dr. John Murray has given an interesting historical account of oceanography from the earliest times, illustrated with a series of maps representing the growth of geographical ideas.

The ingenious arguments founded on neither experiment nor observation, which were indulged in up to last century as to the depth of the sea, etc., are typical of all other early ideas on the subject. Even while the mapping of trade routes was in an advanced state of development, knowledge of the ocean remained strictly superficial. Cook's First Voyage (2) in the *Endeavour* (1768-71), carrying Sir Joseph Banks and Dr. Solander as naturalists, marked the beginning of true observation of the sea. The *Journal* kept by Banks on this voyage, recently edited by Sir Joseph Hooker, has made known to us the fact that Banks was no mere gilded patron of science, but a genuine hardworking observer of nature who did not confine his work to the lands visited, but was incessantly occupied with the marine fauna and flora of the high seas.

The circumstances under which the *Journal* has at length been published after more than a century in one limbo or another, are extremely interesting. At one stage



of its history the original MS. came into the hands of Sir Joseph Hooker's grandfather, Dawson Turner, the celebrated phycologist, who had a copy made for him. While on a visit to his grandfather in 1833, Sir Joseph saw it being copied, and, in assisting to verify the transcript, naturally became fascinated with the story. After other adventures it reached the Manuscripts Department of the British Museum with some eventual condition of its becoming the property of the Trustees. Mr. Carruthers, then Keeper of the Department of Botany, succeeded in obtaining the Dawson Turner transcript for that Department, and in faithfully clinging to it. The original Banksian MS. and correspondence, however, were claimed from the Manuscripts Department in 1885 or 1886, on what appear to be slender grounds, by the late Lord Brabourne, who carried them off, and after some correspondence he declined the sum offered by the Museum for purchase of the Banksian MS., broke up the whole into lots and sold them at Sotheby's, the original MS. of the *Journal* going to an autograph dealer for £7 2s. 6d., whereupon it soon disappeared. This barely credible and discreditable story is told here, and no one can envy Lord Brabourne his reflections on receipt of this paltry sum for a document of national interest. The Dawson Turner copy in the Department of Botany has therefore been the means of saving the *Journal* from oblivion, and it has been used in Sir Joseph Hooker's edition. Besides giving us a fascinating account of Cook's momentous voyage, of such imperial importance to Britain, the *Journal* presents us with a picture of a naturalist's occupation on such an expedition, and of his work at sea. Banks' interest in marine life begins with his leaving Plymouth, and he faithfully records his observations, many of them at that time novel, as he proceeds. He gives, among other noteworthy entries, a good description of the banks of pelagic *Oscillatorieæ*, the "sea-sawdust," seen by him on the coast of Brazil, Torres Straits, and other places. "It was formed," he says, "by innumerable small atoms, each scarcely half a line in length, yet, when looked at under a microscope, consisting of thirty or

forty tubes, each hollow and divided throughout the whole length into many cells by small partitions, like the tubes of *Confervæ*. . . . A Portuguese, who came on board the ship at Rio de Janeiro, told me that at San Salvador, on the coast of Brazil, where the Portuguese have a whale fishery, he had often seen vast quantities of it taken out of the stomachs of whales or grampuses." When one remembers the minute size of the individual tubes and the kind of microscope Banks must have had, the description is marvellously accurate. This observation as to a Protophyte being found in quantity in the stomachs of whales is interesting in connection with the name of "whales' food" given to the masses of diatoms in the Arctic Seas. It was pointed out by the late Mr. R. Brown (Campst.) in 1868 (*Trans. Bot. Soc. Edin.*, vol. ix.) that the well-known discoloration of tracts of the Arctic Sea is owing to diatom life—principally the diatom now known as *Thalassiosira Nordenskioldii*. He found this and other diatoms in the intestinal canal of the small Entomostraca, Pteropodous Mollusca, Medusæ, etc. (the true whales' food), which frequent the discoloured tracts, and in turn live upon the diatoms. Thus it comes about that organisms, which individually are invisible without a high power of the microscope, ultimately furnish the food of the mightiest animals on our globe. In the Antarctic Seas the whales feed on minute animals closely allied to those of the Arctic, and these without doubt also subsist on the extensive tracts of diatoms of the southern ocean with which Sir Joseph Hooker himself, as it happens, first made us acquainted. The whales must inevitably swallow large quantities of the diatoms themselves in pursuit of the minute animals, as was probably the case with the whales mentioned by Banks, and it is possible that the mixed animal and vegetable diet may be beneficial. This observation of Banks is cited merely as showing the living interest his *Journal* possesses to students of the sea at the present day. There are few pages of it that do not show him to be, as Sir Joseph Hooker truly says, "the pioneer of those naturalist voyagers of later years, of whom Darwin is the great example".



Cook, on the conclusion of his voyages, left little to be done in the way of discovering new lands, and gradually attention came to be given more particularly to the scientific study of the sea. Just as Banks was the first notable observer of animal and plant life on the high seas, so the physical study of the sea may be said to spring from Cavendish's self-registering thermometer, first made about 1757. He suggested that it might be applied to ascertaining "the temper of the sea at great depths". Irvine, who accompanied Lord Mulgrave to the Arctic regions, so applied it in 1773 (two year after the return of the *Endeavour*), and he also seems to have invented a water-bottle. On this voyage, also, one of the earliest attempts at deep-sea sounding was made, the greatest depth reached being 683 fathoms. Improvements in apparatus were made, and many experiments were tried in the succeeding years. Franklin, Sir John Ross, and among naturalists the great Ehrenberg were conspicuous by their labours. Sir James Clark Ross's Antarctic Expedition (1839-43), and at the same time Captain Wilkes, who commanded the first purely scientific expedition sent out by the United States, made notable advances. The one expedition was fortunate in carrying Sir Joseph (then Dr.) Hooker, the other Dana, as naturalist. However, after all was done, there was still lacking the material for any important generalisation. Edward Forbes, Captain Spratt, Maury, and many others continued to amass observations and to attract attention to the study by theoretical views of profound interest. Captain Dayman, who sounded across the North Atlantic in H.M.S. *Cyclops* (1857), brought home soundings in which Huxley discovered the Coccoliths. It was not, however, until submarine telegraphy came to be a necessity that any great opportunities came for a systematic study of the deep sea, just as ocean commerce has led to the careful charting of coasts and shallow seas. In 1860 H.M.S. *Bulldog* made a survey for a telegraph route between England and America. It was on this voyage that Dr. G. C. Wallich made his celebrated observations on the existence of a special deep-sea fauna. Many of his opinions have been confirmed by

subsequent researches, and they exhibit an industry and insight of a wholly remarkable character. His discoveries were followed up by Torell, Pourtalès, Agassiz, Wyville Thomson, Carpenter, Gwyn Jeffreys and others, until the *Challenger* Expedition became a necessity. This expedition and the publication of the fifty magnificent volumes of results are a monument of what the British Government has done, and can do, for science. It is being so constantly dinned into the ears of the tax-paying public that our Government does nothing for science, but leaves its advancement almost solely to private enterprise and the Universities, that national pride is apt to fall to zero in the matter. National scientific institutions like the Royal Navy, the British Museum, Greenwich Observatory, Kew Gardens, are always with us in their pretended poverty, and it is significant of our national habit of grumbling that Dr. John Murray in his preface to this concluding volume of the *Challenger* Reports feels it a sacred duty to say that: "The majority of the authors of the special memoirs have spent years in the examination of the collections and in the preparation of their manuscript and illustrations for the press, without other remuneration than either a copy of the *Challenger* publications or a small honorarium to cover the outlay necessitated by their researches. The payments to the Civilian Staff have been very moderate, and in my own case, at least, have not covered actual expenditure in connection with the work of the Expedition." He tells us that, in 1889, the Treasury declined to ask Parliament to renew the annual grant, and after correspondence in which Dr. Murray offered "to finish the Report at my own expense," the Government granted £1,600 for the completion of the volumes, and somehow they have been completed. Dr. Murray has happily survived these privations, and appears in all respects as if they had done him good. Moreover, it would have been a pity if the Treasury had not been true to itself in the course of this great undertaking.

These final volumes contain besides the historical sketch (the substance of which ought to be republished



as a hand-book, together with a brief account of the results of the *Challenger* Expedition) a detailed summary of results obtained at all the observing stations, making a scientific log of the voyage as well as an index to the special memoirs. The summary occupies the main part of the two volumes, and is illustrated with a series of valuable maps and sections. Following the summary is an analysis of the bathymetrical and geographical distribution, itself a gigantic labour, an index of the genera and species, and a general index. These are labours the outcome of which will appear only when years of reference to them will have proved their value. The present interest lies in the much too brief general observations Dr. Murray permits himself to make. One result that was perhaps little expected is that only a relatively small percentage of deep-sea animals have a wide distribution over the floor of the ocean. Alexander Agassiz, as the result of work with closing tow-nets in the *Albatross* so recently as 1891, concludes that "in the open sea, even when close to the land, the surface pelagic fauna does not descend beyond a depth of 200 fathoms, and that there is no intermediate pelagic fauna living between that depth and the bottom, and that even the free swimming bottom species do not rise to any great distance, as we found no trace of anything within sixty fathoms from the bottom, where it had been fairly populated". He thinks, however, that "in a comparatively closed sea, at a small distance from the land, there may be a mixture of the surface species with the deep sea bottom species". Dr. John Murray, however, states that: "The tow-net experiments carried out on board the *Challenger* during several years in all parts of the world led me to the conviction that these intermediate regions were inhabited, although with a much less abundant fauna than the waters near the bottom or those near the surface of the ocean". It is plain that there is here a field for future experiment and observation, especially when a trustworthy closing tow-net shall have been invented,—a simple one that may be used without waste of time and temper. Dr. Murray proceeds to contend that the organisms obtained

by the *Challenger* Expedition from the intermediate depths appear to have a much wider horizontal distribution than the surface fauna, and that they obtain their food by the capture of the dead organisms continually falling from surface to bottom. Agassiz will certainly have some difficulty in meeting his final argument. "It is well known that the deposits at the bottom are in most regions chiefly made up of the dead shells and skeletons of surface organisms. We have no definite ideas as to the rate at which these surface creatures may be falling to the bottom, but it is evident that nets which have been dragged in these intermediate depths on the opening and closing principle, without capturing any of these falling organisms, have either not been dragged for a sufficiently long time and through a sufficiently great extent of water, or have not worked successfully." Those who have not themselves invented opening and closing tow-nets, but who have yet worked with them, will recognise the force of the last four words.

The exploration of the sea has proved to be of exciting interests to geologists. The mere mention of the subject of the "permanence of continents" causes angry passions to rise. It is more than probable that there are yet "crowns to be broke" over this momentous discussion. L. Agassiz thought, so long ago as 1869, that the present continental areas within the 200 fathom line, as well as the oceans, have preserved their outlines and positions from the earliest times; that they have "remained essentially the same through all geological ages, varying only as to their relative height and depth as well as to their respective extension". Passing over the passionate utterances of geologists, which may have all the value claimed for them, we get now the testimony of this other great explorer of the deep sea. Dr. John Murray contends that: "It is most probable that the Ocean Basins were not so deep in these early ages, and numerous islands probably existed in them, with rocks similar to those that now make up the bulk of continental land. Possibly these former land-masses now form the submerged bases of the groups of oceanic islands wholly consisting, so far as we can see, of erupted rocks. In the



gradual evolution of the surface features of the planet, continental land appears, on the whole, to have become more compact, more circumscribed and higher, while the Ocean Basins have become more shut off from each other and deeper. Continental land has been far from permanent, but there are many reasons for believing that the areas on the surface of the planet, within which the present continents are situated, are areas within which continents have been torn down and built up again since the dawn of geological history, while similar revolutions have not taken place in abysmal or pelagic areas of the Ocean Basins to anything like the same extent, and not at all during any of the later geological periods."

Many naturalists besides the authors of the *Challenger* Memoirs have called attention to the striking resemblances between the Arctic and the Antarctic faunas and floras—both littoral and pelagic. So long as there has been climate on the globe, and geologists can point to no trace of it before Mesozoic times, these areas have been separated by the heat barrier of the equatorial zone. It is only fair to suppose that they are derived from a common stock. In an examination of this problem together with the origin of the deep sea fauna, and in seeking an explanation of the fact that the Arctic Ocean was probably a warm coral sea in palæozoic and even later geological times, Dr. Murray brings forward a daring hypothesis, which will no doubt meet with both criticism and ridicule. It has the merit of simplicity, the further one that nobody can deny it, and its spirited author may well ask astronomers and others for a better one. "The waters of these ancient oceans must have had a temperature of 65° or 70° Fahrenheit at the poles," and, "the same temperature and the same marine fauna prevailed from equator to poles, the temperature not being higher at the equator. . . . In early Mesozoic times cooling at the poles and differentiation into zones of climate appear to have commenced, and temperature conditions did not afterwards admit of coral reefs in the polar area. But the colder and hence denser water that in consequence descended to the greater depths of the ocean carried with it a large

supply of oxygen, and life in the deep sea became possible for the first time. There have been many speculations as to how a nearly uniform temperature could have been brought about in sea-water over the whole surface of the earth in early geological ages, as well as to how sufficient light could have been present at the poles to permit of the luxuriant vegetation that once flourished in these regions. The explanation that appears to me the most satisfactory is the one which attributes these conditions to the very much greater size of the sun in the early stages of the earth's history—an idea first introduced into geological speculations by Blandet, who likewise discussed the relations of Arctic and Antarctic faunas—together with the greater amount of aqueous vapour in the atmosphere, and the greater mass of the atmosphere." The pelagic Algæ, Radiolaria and Foraminifera, he holds, are probably the but slightly modified descendants of a very ancient universal pelagic fauna and flora, and life in its simplest form most likely first appeared in Pre-Cambrian times in the detrital matters laid down about the mud-line, when the mud-line was not so deep, and the land surfaces were more extensive than at the present time. These speculations are not stated without a gallant array of facts, and if the style of their exposition be somewhat insistent it is inspired by the fire of enthusiasm. The theory is comforting to the naturalist. Criticism must come from the student of solar physics and from the geologist. It may quite possibly prove that the Arctic fossil coral reefs are mostly, if not all of them, Bryozoa reefs—the point needs further research—and it may be that botanists have accepted on evidence that is not quite so convincing as was formerly supposed Heer's contention that Greenland once had a warm climate,—in short the provocation for Dr. Murray's theory may be less slender, but it is hard in any case to get over the evidence of massive calcium carbonate organic deposits in ancient Arctic seas always associated with warm waters, or the occurrence of veritable fossil tree-ferns like *Dicksonia* in Greenland.

Appended to the second part are two belated special memoirs, that on *Spirula* by the late Mr. Huxley and Dr.



Pelseneer, illustrated by Mr. Huxley's beautiful drawings, and the *Report on Oceanic Circulation*, by Dr. Buchan, with sixteen valuable maps.

Since the return of the *Challenger*, marine exploration has been carried on by the United States ships, *Tuscarora*, *Blake*, *Albatross*, *Gettysburg* and *Enterprise*, the German *Gazelle*, and the *National* or Plankton Expedition under Hensen in the Atlantic, the Norwegian *Vöringen*, the Prince of Monaco's *Princesse Alice*, the Italian *Washington* and *Vettor Pisani*, our own *Knight Errant*, *Triton*, etc., and by the Swedish Government in the Baltic and North Sea. Last of all much is to be expected from the work of the *Fram*. All the ships cited, and many others, have been steadily gathering facts; but to the naturalist perhaps none of them, since the *Challenger*, has gained such a harvest of interesting results, worthily published, as Hensen's Plankton Expedition. It would be out of the question to attempt more than notice of some of the weightiest results recorded in the publications of the voyage. Among those of general interest the researches of Bernhard Fischer (3) and Franz Schütt (4) claim particular attention.

Among the dark places in our knowledge of the economy of the sea there have been until recently two in particular urgently calling for more light. It has been a commonplace reflection of sea naturalists for many years (though Dr. Fisher appears to think it an original idea of Hensen's) that the minute free floating plant life of the sea must furnish the pastures of the animal life of the sea. The crucial observations, to be noticed presently made by Professor McIntosh and Mr. George Murray (7) settle by proof the actual fact of the diatoms affording sustenance to the animals of the sea—a fact long foreseen, but not until recently established in a satisfactory manner. The other crucial point has been determined mostly by Dr. Fischer himself. His early observations on a voyage to the West Indies in S.M.S. *Moltke* (1885-86) and his subsequent work during the Plankton Expedition, taken together with the researches of Russell and others, testify abundantly to the existence of

bacteria in the ocean where they play (as on land) the part of middleman between death and life, by causing the putrefaction of dead bodies of animals and plants—in other words by transforming dead organic substance into simple inorganic combinations to be used by plants and thus restored to the circulation of organic matter. This circulation of organic matter, as we know it on land, has hitherto been only guessed at in the deep, and Dr. Fisher and Messrs. McIntosh and G. Murray have, as it were, completed the two gaps in our knowledge of the circle.

Very little was known of the existence of bacteria in the sea when the Plankton Expedition sailed. Dr. Fischer had made his earlier observations, and after the return of the expedition, and before the publication of his memoir, Dr. Russell<sup>1</sup> made investigations in the Bay of Naples; these with the work of De Giaxa<sup>2</sup> practically exhaust the literature of marine bacteria. That the bacterial contents of the sea are being constantly influenced by the land is a fact beyond doubt. The sea is not only constantly receiving bacteria from the land, but all manner of such substances as nourish bacteria. A very poor estimate can be formed of the numbers carried by the winds to the sea, but we know that the rivers which are, many of them, little better than drains of organic matter are every moment conveying myriads to the sea. Nothing is more astonishing, however, than the rapid manner in which the sea, as it were, disposes of them. De Giaxa and Russell made experiments at varying distances from the opening of the sewer canal at Naples, and they found that at three kilometres from the shore the influence of the land was no longer recognisable. Similar observations made at Kiel, where the haven is more land-locked, gave a slightly different result, but it may be taken as generally true that the coastal waters, often very rich in bacteria near the shore, are generally quite free from the influence of the land in this respect at from three to five kilometres out to sea. Even, however, at places farthest removed from land, bacteria are present as a rule and at

<sup>1</sup> *Zeitschrift für Hygiene und Infektionskrankheiten*, Bd. vi.

<sup>2</sup> *Ibid.*



considerable depths. In 1891 Russell found them on the floor of the Mediterranean itself fifteen kilometres from land at a depth of 500-600 fathoms. Their vertical distribution in the ocean may be summed up as scarce in the surface layers, increasing downward to 100 fathoms, occurring regularly to 200 fathoms, but steadily diminishing from 100 to the depths between 400-600, beyond which they have not been traced with certainty. It appears, moreover, fairly certain that the destructive action of sunlight is the cause of their scarcity at the surface, that they increase with the darkness, and reaching an optimum of general conditions of life at 100 fathoms, decrease again with the lowering of the temperature and the increase of pressure. Bacteria at 500-600 fathoms must undergo a pressure of over 100 atmospheres, and though it is known from experiment that they survive considerable pressures yet the vast pressures of the deep sea may be expected to reckon as a factor in determining their range in depth. Temperature also must play an even more important part. In the Mediterranean, where Russell's observations were made, the bottom temperature is constantly  $13^{\circ}$  C. all the year round, below about 100 fathoms, while above that it varies with the seasons. In the ocean the bottom temperature at great depths is always so low that no development of bacteria could be expected. The bottom of the Atlantic is either extraordinarily poor in bacteria or wholly free from them, the observations not being conclusive. In fact below 400 to 600 fathoms there is no certain record. These are the depths to which one would assign in fact the graveyard of the dead sinking surface plankton. That sunlight is, as every known fact would indicate, the cause of the scarcity in the surface layers is proved further by the fact that the strong light of summer periodically reduces the quantity in the upper waters.

Marine bacteria are moreover of peculiar sorts, though morphologically they resemble their land allies in adopting the well-known globular, rod-like and spiral forms. The luminous forms are confined to the coastal waters for the most part where they are found regularly on fishes, etc.,

and are in fact more abundant on them than in the surrounding waters. The forms peculiar to the high seas are of a very few species, but these have a wide distribution. From the fact of this general distribution and their development on dead animals and plants, Fischer makes the safe inference that they play the great and necessary part of putrefactive organisms in the economy of the sea, keeping the waters from becoming choked with dead organic matter, breaking this up and restoring it to circulation. There is as yet no evidence that the sea bacteria are able to cause diseases in the bodies of marine animals. Inoculation experiments by which the luminous forms caused the death of mice (the bodies of which subsequently exhibited phosphorescence) may be significant or may be misleading just as one is sanguine or cautious. The whole investigation of marine bacteria is yet in its infancy, and comparatively local in its results, but its advancement will undoubtedly throw an interesting light on the general study of these organisms.

Dr. Schütt, who with Dr. Fischer was one of the naturalists of the German Plankton Expedition, has made a minute and careful study of the little-known group of *Peridinieæ* (4 and 5), which form, together with the diatoms, the great bulk of free-floating marine vegetation, especially in temperate regions and near coasts. They are familiar to all from being the source of the luminosity or phosphorescence of our seas in summer and autumn. While diatoms are most abundant in our seas in the spring months, there are very few *Peridinieæ*. In summer and autumn the diatoms, though still plentiful, give place to enormous quantities of *Peridinieæ* which continue fairly abundant until about December, when they wane before the gradual predominance of diatoms again. They are a remarkable group, and our knowledge of their structure is due more to zoologists than to botanists from the rooted disinclination of the latter to use tow-net and microscopes at sea. The shore-loving botanist, however, will have to find his sea-legs before long, since so many problems are being submitted to him by the few who have ventured on the ocean



in search of work. From the researches of Dr. Schütt and several distinguished predecessors, it appears that we must regard the *Peridinieæ* (and some allied minor groups) as related to the diatoms from the structure of their membranes, mode of division, chromatophores, etc. Their membranes are not silicified like those of the diatoms, their valves frequently consist of several plates, their girdles are of different structure, they possess propelling whip-lashes, but in all or most of the points of difference the parts in question are comparable each with each, though the homologies, as Dr. Schütt states them, may appear sometimes a little strained. The new shells or valves of the *Peridinieæ* not being produced within, or overlapped by, the older membranes, they do not steadily diminish like the diatoms, and their life history is therefore not complicated by the production of auxospores. Moreover they appear to play the same part in the economy of the sea, as the diatoms do, in furnishing with them the great bulk of the nutriment for marine animals, the basis of most fishery problems. Dr. Schütt in the latter of the two works cited deals with some of the allied minor groups, such as *Gymnodiniaceæ*, the inclusion of which may be questioned by some authorities. As for *Pyrocystis* (the source of tropical luminosity in many cases) be it a state of *Noctiluca* as Moseley, Bütschli and others have contended, or be it a plant as others still hold, its place is at all events not in *Gymnodiniaceæ*. This part is in several respects the least satisfactory of Dr. Schütt's work, and his treatment of the diatoms (*Bacillariaceæ*) will meet with adverse criticisms from the special students of these organisms. However all owe him thanks for the compendious account of the whole series given in *Engler und Prantl* (5).

Diatoms have so long been a weariness to every naturalist, other than the sect of devotees of their study, from the fact that this study has consisted of mere records of markings and the performances of particular high power lenses mixed with unscrupulous jugglings in the nomenclature of forms, that it is refreshing to come upon discoveries of living interest to cultivated readers of natural

history. Mr. Comber (6) has placed some early observations by Lauder and others together with his own acute investigations, with the result that there is now a firmly established knowledge of the production within diatoms of other forms with different sculpturing of the tiny shells, probably in fact a dimorphism which may or may not occur in alternate order. Mr. George Murray (7), working at sea on the *Garland* on behalf of the Fishery Board for Scotland, independently established the same point by observation of the living forms and carried the matter further. He points out that the internally produced form (dealing with different genera from those of Mr. Comber) may itself multiply indefinitely in the sea before recurring to the parent form, and that not one merely but groups of two, four, eight, or sixteen of such forms may be produced within the parent, and that these are in certain cases not different from the parent but exactly resemble it. These details, important and utterly unexpected though they be, absorb the interest of the botanist more than that of the general student. Just as the great work of Russell, Fischer and others on the Bacteria of the sea has furnished us with a missing link in the chain of economic relationships of organisms, so another such link has been found, or rather strengthened, in Mr. George Murray's observations. Reference has been made to the observations of Mr. R. Brown on the occurrence of diatoms within the intestinal canals of the animals which form the food of whales, and their presence within many sea animals from full-grown fishes downwards is a well-known fact. That the plankton or surface floating plant-organisms are the basis of animal nutrition in the sea has long been obvious, but direct observation has been wanting. Mr. Murray made a minute examination of the substances digested by the Copepoda and other small crustacea, which themselves form a large part of the food of fishes, with the result that he has discovered such substances to consist almost exclusively of the chromatophores or colouring granules and fine fragments of the siliceous shells of diatoms. Professor McIntosh anticipated this observation, having made a brief record of the



fact without details in an account of other matters in a previous Fishery Board Report. Search was made by Mr. Murray for evidence of these animals eating *Peridinieæ*, but without success, possibly owing to the more easily destructible character of these organisms within the digestive tract, probably to their escape in many cases from being devoured by reason of their frequently spiny character. This seems to be the more likely since he failed to discover traces of spiny diatoms being eaten, and the beautiful sculpturing of diatom shells may come to be reckoned with the thorns and prickles of land plants as defences against animals! That young fishes themselves eat diatoms appears to be the case. He took young sand eels, young flat fishes and young clupeoid fishes, and reduced them to a fine ash which was found to contain considerable quantities of different diatoms, not broken as they would have been had they been eaten previously by small crustacea. Whitebait would appear from these experiments to be worthily fed on the beautiful diatom *Coscinodiscus*. As "all flesh is grass" in the strictly physiological sense, so all fish appears to be diatom. These organisms hitherto known to us as yielding the material for dynamite, polishing powders, and the amusement of harmless old gentlemen with microscopes, must in future be treated with becoming respect.

It undoubtedly represents an advance in methods of work when a fast mail steamer can be converted into a plankton expedition by simply taking a passage on board of her and pumping sea water from the deck hose through a fine silk bag and retaining the filtered substance for examination. Messrs. Murray and Blackman (9) have done it even more economically by capturing Captain Milner of R.M.S. *Para*, providing him with the apparatus and a little instruction, and sending him forth to look in the Atlantic for objects requiring an immersion lens to disclose their appearance.

By this means they obtained for study not only the Coccospheres and both kinds of Rhabdospheres, but *Pyrocystis* as well—a remarkable haul of debateable organisms. Their examination of them, briefly recounted, tends to confirm the view taken of them in the "*Challenger*" Narrative,

but evidence of their actual plant characters is yet incomplete and must remain so until competent observers have studied them alive. However, after the doubts thrown on the very existence of the Coccospheres and Rhabdospheres by the Hensen Expedition it is refreshing to find our countrymen vindicated. Captain Milner certainly deserves congratulation on having accomplished in a mail steamer, keeping contract time, what a thoroughly equipped German National Expedition failed to effect.

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GEORGE MURRAY.



## THE VENOMS OF THE TOAD AND SALAMANDER.

**B**OTH in ancient and modern times a belief in the venomous nature of the toad and of the salamander has been almost universal, and many passages referring to this are to be met with in the writings of Aristotle (B.C. 332) Theophrastus (B.C. 322) Pliny and Dioscorides (A.D. 79). Shakespeare also alludes to it in several places, for example, a toad which had “sweltered venom sleeping got” was the first, and hence presumably the most important of the ingredients in the Witches’ Cauldron in “Macbeth”. Pliny is especially emphatic with regard to the salamander—“of all venomous beasts there is none so hurtful and dangerous as the salamander,” and he goes on to say that the venom is narcotic and resembles aconite in its action. Until quite recently, if not at the present time, there was a popular idea in the West of England that a dog which worried a toad became mad.

The toad formerly had a place in the *materia medica*—in Spielman’s *Institutiones Materiæ Medicæ* (A.D. 1784) two preparations are mentioned, “*bufones exsiccati*,” dried toads, and “*cineres bufonum*,” ashes of toads, the former being described as useful in bleeding from the nose and the latter in dropsy. The employment of preparations of the toad as remedies for dropsy is not so absurd as may at first appear, for it will be seen later that a substance is secreted by the skin very like digitalin, and hence possibly having a favourable effect in cases of cardiac dropsy.

Fact is often as strange as if not stranger than fiction, and the result of a number of investigations will be found to confirm the traditions mentioned above, much as they have been derided. If a toad (*Bufo vulgaris*) or a salamander (*Salamandra maculosa*) be examined, it will be found that the dorsal region and limbs are studded with numerous warty prominences, and in the toad there is also a large elongated gland on either side of the neck which has been

termed the parotid gland. These are the "venom glands" and their secretion, the "venom," is a white milky fluid, intensely bitter and somewhat acrid to the taste, which exudes on pressure, on electrical stimulation, or after death by chloroform narcosis; in the latter case every gland will be found to be tipped by a white milky bead of the secretion.

Several observers (1) have studied the histological characters of these glands, which, as they have essentially the same structure in each animal, may be described together. The gland follicles are more or less globular and communicate with the surface by a short duct. The lining membrane of the larger follicles is thrown into folds forming imperfect septa which project into its cavity and are covered with a flattened epithelium. In the smaller follicles these septa are wanting, and the lining epithelium is more or less cubical. The walls of the follicles are plentifully supplied with nerves and blood-vessels.

That these cutaneous glands in both the toad and salamander really do secrete a venom which is extremely toxic when introduced into the circulation is acknowledged by, and is moreover conclusively proved by the experiments of, all investigators with the exception of Davy (2 and 3) and Rainey (1) who failed to observe any ill effect from the secretion of the toad, their failure being due perhaps either to the administration of too small a quantity of the venom, or because of its non-absorption into the circulation, probably the latter. The production of venom is by no means confined to the common toad and land salamander, but is met with in allied species,—the natterjack and tropical toads, the tritons, and to a small extent the frogs. The creatures are unable voluntarily to eject the venom, which is secreted only in response to some reflex irritation and has a purely defensive function.

Pelletier (4) in 1817 appears to have been the first to investigate chemically the venom of the toad. He found that it was acid in reaction and partially soluble in alcohol. A fuller examination was made by Davy (2) in 1826 who describes it as a yellowish thick fluid the greater part of



which is soluble in water and in alcohol, its solution not precipitated by lead acetate and only slightly by corrosive sublimate, and giving a purple colour with nitric acid; the alcoholic extract being "very acrid, acting on the tongue like extract of aconite".

Gratiolet and Cloez (5) in 1852 by treating the dried venom with ether, evaporating the ethereal solution and extracting the residue with alcohol, separated the active principle more or less completely and found that it was entirely soluble in water acidified with hydrochloric acid, this solution being precipitated by bichloride of platinum and by corrosive sublimate. They considered that these and other facts seemed to establish the probability of the existence of an alkaloidal substance in the venom. Twenty years later their surmise was proved to be correct by Casali and Fornara (6) who succeeded in extracting by the Stas-Otto process an alkaloid to which they gave the name of phrynine or bufidine and possessed of the following properties—a white amorphous solid, slightly soluble in water and very soluble in alcohol, ether and chloroform. It gave precipitates with picric acid, platinic chloride, and iodic acid, but not with lead acetate (*cf.* Davy) nor with potassium ferrocyanide and acetic acid. They were unable to ascertain its percentage composition, as the amount of material at their disposal was limited. Calmels states that the venom of the toad contains methylcarbylamine and isocyanacetic acid (7).

The writer has recently examined chemically the cutaneous secretion of the toad. It is a thick milky fluid, acid in reaction, drying quickly in the air, forming a yellowish amorphous solid almost completely soluble in alcohol but only partially so in water, the solution being very bitter. The secretion and glands from several toads were placed in absolute alcohol where they remained for some time, the alcoholic solution was then filtered off and evaporated, and yielded a greyish amorphous residue which was slightly soluble in distilled water and more so in water acidified with hydrochloric acid. The solution gave precipitates with iodine in potassium iodide, gold trichloride, platinum bichloride, Nessler, and picric acid, the latter one dissolving

completely on heating and reappearing on cooling, it gave no precipitates with mercuric chloride, cupric sulphate, ferric chloride, and potassium ferrocyanide and acetic acid. These reactions indicate the presence of an alkaloid and the absence of any proteid body. The solid residue gave an orange-brown colour with sulphuric acid, an inky-brown colour with nitric acid, a reddish colour with sulphuric and nitric acids, a brown becoming purplish with sulphuric acid and a trace of bromine, and a greenish colour with hydrochloric acid on warming. These reactions are not unlike those yielded by digitalin.

The first observation on the chemical nature of the venom of the salamander seems to have been made by Gratiolet and Cloez in 1851 (8). They describe the venom as being a whitish milky fluid possessing a strong penetrating and disagreeable odour, acid in reaction, coagulating quickly on exposure to the air and instantly on the addition of alcohol: in this it differs from the venom of the toad. A little later Vulpian gave a similar account of it (9). Zalesky in 1866 (10) made a very complete examination of this venom and succeeded in extracting an alkaloidal body. The venom was diluted with water, heated, filtered to separate a coagulum, and the filtrate precipitated by phosphomolybdic acid. The precipitate was dissolved in baryta water, the barium precipitated by a current of carbon dioxide gas and filtered off, and the filtrate concentrated over a water-bath in a current of hydrogen. Long needle-shaped crystals were obtained which on complete drying formed an amorphous mass soluble in water and giving an alkaline solution which was precipitated by phosphomolybdic acid and by platinic chloride. The composition of this alkaloid is expressed by the formula  $C_{34}H_{60}N_2O_5$  and its hydrochlorate by  $C_{34}H_{60}N_2O_5 \cdot 2HCl$ . Zalesky named it Samandarine (from the Persian Samandar, whence Salamander), but subsequent writers have invariably termed it Salamandrine. It will be evident from the foregoing that the active principles of the venoms under consideration are totally different substances from those of snake venom, the former being alkaloidal while



the latter are proteid in nature (11). Both venoms have a special action on the nerve centres. Gratiolet and Cloez (8) found that 2 milligrams of the dried venom of the toad when injected subcutaneously killed a greenfinch in fifteen minutes with convulsions and loss of co-ordination. Vulpian (12) and later Couty (13) observed that this venom when placed in a subcutaneous wound was fatal to dogs and guinea-pigs, but when administered by the mouth produced nothing more serious than vomiting, the fatal event in the former case being preceded by excitement and vomiting and sometimes by convulsions. Placed in contact with the skin of frogs and tritons it is absorbed and kills them in from two to three hours (14).

Fornara (15) has shown that phrynin has an action on the respiration and circulation very like digitalis, it induces contraction of the arterioles and rise of blood pressure, increased cardiac contraction and diuresis. According to Phisalix and Bertrand (16) the blood of the toad is toxic from the presence of some of the active principle phrynin; 2 c.c. injected into a frog begins to produce symptoms within five minutes, and in fifteen minutes the pupils are contracted and hind legs paralysed, while 5 c.c. quickly kills a guinea-pig.

The venom of the salamander differs from that of the toad physiologically by its predominant convulsive action and by its inactivity on the heart. In the experiments of Gratiolet and Cloez (8) small birds such as chaffinches inoculated with it suffered from epileptiform convulsions, and paralysis followed by death in from six to twenty-six minutes; but mice and guinea-pigs though severely affected ultimately recovered. Vulpian (9) found that the venom was fatal to dogs in from two to three hours, to guinea-pigs in nine hours, and to frogs and toads in five hours. Its action on frogs was studied by Roth (17): convulsive movements are first induced, followed by paresis and paralysis of all voluntary movements. The heart's action remains normal for several hours after the cessation of all voluntary and reflex action.

Zalesky (10) observed that salamandrine produced

tremor, epileptiform convulsions, opisthotonos and death, and later experimenters have generally used this alkaloid or its hydrochlorate. According to Phisalix (18) the minimal fatal dose of the latter administered by subcutaneous injection is for the mouse  $\frac{1}{10}$  of a milligram and for the dog about 1.8 milligrams per kilogram of the body weight. Intravenously the poison acts rapidly and in smaller doses. By the mouth the dose has to be much larger, for example, administered in this way, 10 milligrams on the mouse and 20 milligrams on the guinea-pig has little effect, and on the dog to produce appreciable symptoms the dose has to be increased to 8 milligrams per kilogram of the body weight. An interesting point is that when given by the mouth the fresh venom is more active than the hydrochlorate of the alkaloid.

Phisalix and Langlois (19) exhaustively studied the physiological action of salamandrine. The earliest symptoms of poisoning in the dog are restlessness, salivation, vomiting and tremor. Convulsions soon follow during which the temperature rises rapidly, the respiration being affected solely as a part of the general muscular spasm during their occurrence. It has no direct action on the heart though the vaso-motor system may be implicated to a slight extent. The post-mortem appearances are congestion of the principal viscera, hæmorrhagic points in the diaphragm and heart muscle, and emphysema and hæmorrhages in the lungs. The meninges are congested and the pia mater of the fourth ventricle is studded with hæmorrhagic points.

Many other interesting features in the action of the venom have been observed by Dutartre (20). Salamandrine, unlike the active principle of the toad's venom, is not found in the blood nor is it present in the tadpole. The venom has little or no action on the snail and slug, in crickets it produces convulsions followed by a lethargic state which passes off in about twenty-four hours and the insects recover, while not only are bacteria unaffected but they live and multiply rapidly in an aqueous solution. In some mammals and in frogs the venom produces a considerable



diminution in the number of blood corpuscles, rapid abolition of muscular contractility with paralysis, sensation however persisting.

By daily injections of increasing doses of salamandrine, commencing with a non-lethal one, an animal can be rendered immune so that it is unaffected by an amount which would prove fatal to an untreated animal. For example, Phisalix (18) gave a young dog weighing 2 kilograms subcutaneous injections increasing from a  $\frac{1}{4}$  of a milligram up to 4 milligrams during a month without producing any ill effect. A control animal weighing  $2\frac{1}{5}$  kilograms was then injected with 4 milligrams and died at the end of twenty-four hours with the characteristic symptoms.

Another fact of interest is that with both the toad and salamander the venom is fatal to the animal which secretes it only in comparatively large amounts. Thus the last-named author found the lethal dose of salamandrine for the salamander to be from 5 to 10 milligrams subcutaneously, that is a dose from 50 to a 100 times greater than suffices to destroy a mouse. Vulpian (9) made a similar observation with regard to the toad and ascertained that the venom of each of the various species is toxic to the remaining species, though all have a general similarity in action—for instance salamandrine is fatal to toads and tritons in ordinary doses, the venom of the toad is fatal to tritons and *vice versa*, while the venoms of the toad and triton poison the salamander (21).

The secretory apparatus of the venom glands is governed by a nervous mechanism, the centres for which are located in the optic lobes as was shown by Phisalix and Contejean (22). Muscarine, strychnine and ammonia excite secretion, while cocaine, eserine, and morphine inhibit it. It was incidentally noticed that the salamander is remarkably refractory to certain poisons, it is only completely curarised by 43 milligrams of curare while morphine is apparently quite inactive. The interesting fact was demonstrated that the salamander's blood and blood-serum act as an "antitoxin" towards curare (23). The following experiments illustrate this—20 parts of the defibrinated blood were mixed with  $1\frac{1}{2}$  parts of a 1

in 1000 solution of curare and injected into the peritoneum of a frog, while as a control 20 parts of salt solution mixed with the same amount of curare were injected into another frog, this latter was completely curarised in ten minutes, while the former one was unaffected. In other experiments the serum was first injected into frogs and the curare subsequently. Thus a frog received 1·3 c.c. of serum and the following day 0·39 milligram of curare, six times the lethal dose, without showing any symptoms. It was ascertained that 0·4 c.c. of serum just neutralised the minimal fatal dose of curare (mg. 0·065) for the frog.

This summary suffices to show that the belief of the ancients in the venomous nature of the toad and salamander was not altogether devoid of foundation. The appearance of these creatures and the peculiar sensation experienced on handling them, to many most repulsive, together with their shy, retiring habits, would favour an evil repute in an age when Nature was not studied as she is now and before the advance of scientific investigation and the growth of individual culture had banished superstition and ignorance.

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## THE RED PIGMENT OF FLOWERING PLANTS.

GREEN is the fundamental note in the colour symphony of plants ; but red is of frequent recurrence. The green colour is due to a mixture of pigments called chlorophyll held in the meshes of protoplasmic bodies capable of growth and division, termed plastids ; the red, of the foliage of higher plants, is caused by a colouring matter known indifferently as anthocyan or erythrophyll which is dissolved in the cell sap. With another red pigment, phycoerythrin, which gives the characteristic colour to the group of algæ, the Florideæ, and which is associated with chlorophyll in the plastid, this paper is not concerned.

The part played by the green pigment chlorophyll in the economy of plants is well known ; but the *rôle* of the red colouring matter is obscure and the subject of much guess-work. Since, however, some experimental researches have recently been directed to the elucidation of the question, it seems not inopportune here to summarise what is known concerning the properties of this red colouring matter.

The colouring matters, soluble in water, which are contained dissolved in the cell sap of many plants are, by some, termed collectively anthocyan, or, more objectionably, erythrophyll (1) ; by others, they are referred to two groups, the reds, blues and blue-greens to the Anthocyanin or Cyanin (2) group ; the yellows and yellow-browns to the Anthochlorin or Xanthëin group. As will be seen, the chemical nature of these pigments is unknown and consequently any complicated terminology premature. Opinion is divided as to whether the red and blue pigments are in reality identical, the respective colours being due to acidity or alkalinity of the cell sap, or whether they are different chemical bodies. Krukenberg, (3) in his comparative



physiology of colours and colour bodies, seems to regard these various pigments as identical, stating that the blue and violet pigments are converted by acids to reds; and the reds by iron sulphate and by sodium phosphate to violet; by saturation with sodium salts to blue; by the action of alkalis, a red solution becomes green and neutralisation by any acid revokes the original red. Hansen (4) too, relying on his spectral analyses of red and blue pigments prepared from various members, believes in the identity of the variously coloured pigments. N. J. C. Müller, (5) on the other hand, claims to show, in the case of flowers, a much greater variety of pigments than is generally thought to exist. He examines the substances in question before treatment with special reagents and after the action of sulphuric acid and of potash. By the action of potash on various red pigments he obtains a series of derivative colours, blue, blue-green, yellow, brown and green. Müller does not state, however, how his original solutions are obtained; and so at present it must be left doubtful as to whether the red and the violet pigments dissolved in the cell sap, or even the reds from different plants, are of the same or of different chemical composition.

Concerning the origin of these colouring matters, which for convenience may at present be termed collectively anthocyan, our knowledge is a little more exact. In the first place, there seems to be no question that they are *not* derived from chlorophyll. For, not only does red-coloured sap occur in the cells of young tissues before chlorophyll is developed, and also in the cells of various phanerogamic parasites (devoid of chlorophyll) as *Balanophora*, *Rafflesia* and the *Hydnoreæ*; but also Hansen (6) describes in the leaf parenchyma of species of aloe, a colourless chromogen which, acted on by water and oxygen, gives rise to a red pigment similar to that contained in many fruits. Like chromogens are probably to be found in many of those colourless underground parts of plants, such as the rhizomes of *Dentaria bulbifera*, *Viola* sp., etc., which become violet coloured on exposure to light. Wigand (7) has shown that red sap is peculiarly characteristic of tannin-containing

plants, and that the pigment of this sap arises from a colourless highly refractive substance giving tannin reactions. Kraus and Detmer (8) also hold the view that the reds appearing in the autumnal coloration of leaves, in so far as they are due to substances dissolved in cell sap, also originate from tannins. Pfeffer, (9) on the contrary, states that in no case has this origin been actually proved. Kutscher (10) and more recently Pick (11) claim to have demonstrated the transition from tannin-reacting substance to red pigment in many flowering plants. The latter author describes a large number of cases of developing shoots whose cells, which a little later are filled with red sap, abound in a colourless, refractive, tannin-reacting substance, the disappearance of which is followed *pari passu* by the advent of the red pigment.

It has long been known that external conditions exert an important influence on the production of the red colouring matter. Senebier (12) observed that, in fruits partially covered by tin foil, the red is only developed in the areas exposed to the sun. Von Mohl notes in his *Vermischte Schriften* that the red colour is called forth by illumination, and that a low temperature favours its appearance. Landel (13) has investigated the influence of light more completely, and finds that variations of the intensity of the sun's rays act uniformly, but in varying degrees, on the production of red colours in stems and other parts.

Sachs' (14) classical experiments, by which he found that the colours of flowers are developed in the dark—albeit, according to Askenasy (15), more feebly than in the light—and also the facts that red sap may occur in dark grown and underground parts, indicate, unless we suppose here a prolonged after-effect of light, that external conditions influence the amount of formation rather than the actual formation of the pigment.

It may be well here to enumerate the chief localities in which anthocyan may occur, in order that the intricacy of the problem of its physiological significance may be borne fully in mind. The following is largely based on Frank's classification :—



*Temporary Red Coloration.*

1. Young developing shoots: common in temperate regions; very characteristic of trees of hill country of tropics.
2. Autumn leaves during depletion.
3. Grown green leaves during cold weather of spring or autumn (red on light-exposed side):

*Temporary or Permanent.*

4. Stem, leaf-stalk and mid-rib becoming red in sunny places, not in shade.
5. Wounded or weak places of leaves and fruit (neighbouring sound tissue often red).
6. Alpine plants.
7. Plants of deep shade (specially within the tropics).

*Permanent.*

8. As a phenomenon of variation.

From this summary it will be clear, how grave is the difficulty of ascribing to anthocyan any single consistent function, and how tempting it is to apply the neo-teleology of adaptation to each case. The pursuit of this doctrine of the obvious has been followed by none more keenly than by Kerner (17), who supplies a significance for nearly all the different occurrences of anthocyan. His statements, in some cases supported by experiment, are as follows. To the anthocyan occurring in the under side of leaves, *e.g.*, in floating leaves and those of shady forests, and in the non-chlorophyll containing parts of Alpine plants, he assigns the function of a converter of light to heat, by which means the metabolic processes of the plant may be conceived to be facilitated: transpiration, for example, being augmented. In seedlings, developing in spring or in cold weather, the anthocyan appearing promiscuously in the leaf, but mainly along the veins and on the leaf stalk, assists, according to him, the translocation of carbohydrates by keeping back light which he states to be inimical to this transport. Lastly, the

anthocyan occurring in the upper epidermis of many Alpine plants, and which he finds is the more developed the more intense the light, Kerner regards as a protective screen to chlorophyll.

It is seen then that anthocyan, in its time, plays many parts. The last-mentioned screen theory may be first considered. Kerner supports his view by interesting observations on the growth of plants in Alpine (Tyrol) regions. He finds, for example, that *Satureja hortensis* flourishes at heights of 2195 metres, and he attributes this to its power of forming large quantities of screening anthocyan. Flax, on the other hand, grows well at 1500 metres, but turns yellow and dies at 2195 metres. Could flax manufacture anthocyan like *Satureja*, Kerner adds, it would blossom and fruit like it. Kerner attributes the death of the flax to the destruction of its chlorophyll, which, in the case of *Satureja*, he assumes to be screened by anthocyan. But this inference is hardly justifiable. It is true that Pringsheim (18) showed long ago that intense artificial light destroyed the green-colouring matter of living plants, and indeed in some cases destroyed the protoplasm itself. Wiesner (19) similarly has brought experimental evidence to show that chlorophyll may be destroyed by too intense sunlight. Other observers have expressed themselves in the same sense (20). Johow (21), for instance, states his belief that the action of light on chlorophyll is indirect, and takes effect especially in young and in shade-loving members. So that although some writers, such as Stahl (22), do not attach great importance to this destroying action of sunlight, it may be conceded that too intense insolation is a source of danger to the plant.

This general truth, if general truth it be, is not sufficient to make Kerner's interpretation of his results justifiable. For Pringsheim (23), and in more recent times Marshall Ward (24), have shown that the destructive action of light commences in the region of the blue-green, and rises to a maximum in the violet. Till the precise spectrum of the pigment in *Satureja* be examined, it cannot be affirmed that this body is capable of acting as an efficient absorbent



medium for the toxic rays. It may be confidently stated that ordinary anthocyan obtained from various plants would be by no means serviceable in this respect, as the curves of anthocyan absorption figured by Engelmann show, and as will be readily understood when the absorption spectrum of anthocyan is later described. It is true that violet cell-sap absorbs more of the violet end of the spectrum than does red-coloured anthocyan, but even this colouring matter intercepts still more of the red end of the spectrum than of that rich in toxic rays.

The screen theory must then, for the present, be regarded as non-proven. Stahl has criticised Kerner's view very adversely. He inclines to the belief that too much weight has been attributed to the destructive effect of light on chlorophyll; whereas the thermal effects, helpful or harmful, have not received sufficient attention. He adds the further criticism that, before Kerner's conclusions from his Alpine experiments can be accepted, other researches must be made, some at still higher altitudes, others in which some of the plants are protected at night; for as will be seen when Stahl's own work is considered, the death of the *Linum* plants may be due to a cause other than that of too intense light. The consideration of the other two of Kerner's conjectures concerning the functions of anthocyan may be postponed till the researches, in which they are respectively re-stated are discussed.

The absorption spectrum of the red-colouring matter of leaves has been very fully investigated by Engelmann (25). He finds a general agreement in this respect between the red pigments of different plants. The absorption by these red pigments is greatest in the green but extends as far as the D line on the one side and beyond F, although here very feeble, on the other; beyond G again there is some little absorption. Thus the absorption spectrum of anthocyan is practically the reciprocal of that of chlorophyll. Engelmann remarks that in many plants the chlorophyll grains live permanently behind red screens of such absorbent power that  $\frac{1}{3}$  to  $\frac{1}{2}$  of the total light is absorbed, without assimilation being in the least impaired.

In passing, it is interesting to note that Engelmann sees in these facts a confirmation of his important assertion that the amount of assimilation effected by light of a certain wave-length is proportional to the degree in which that wave-length is absorbed by chlorophyll; and he draws attention to the fact that the above observations do not so well fit in with the older view that the maximum assimilation is effected by yellow light, in as much as anthocyan effects some considerable absorption of that light. As to the positive significance of anthocyan, Engelmann is silent.

A paper by Pick (26), dealing specially with the significance of the red-colouring matter of Phanerogams, has given rise to much discussion. This author confirms Engelmann as to the absorption spectrum of anthocyan and finds that the nearest approach to a substitute for the red sap is afforded by a solution of alum-carmine and next by ruby glass. Pick concludes from his experiments that the red colouring matter of leaves has the function of, in the highest degree, facilitating carbohydrate translocation, without interfering with the assimilatory activity of chlorophyll. This function of anthocyan may be conceived to be of great importance. For, from experiments of Sachs (27) and others, it is known that in many plants the amount of carbohydrate manufactured by the leaf during the day is in excess of the amount which diurnally passes as sugar from the leaf. The carbohydrate not immediately translocated takes the form of starch and as such is stored by the leaf. This residue of the carbohydrate manufactured daily is, during the night, converted by diastase into sugar and in this condition passes from the leaf. In places subject to very cold nights this nocturnal work is liable to be both dangerous and ineffectual; dangerous since it may prevent the protoplasm of the leaf from passing into a resting condition when low temperature would do comparatively little harm; ineffectual since at low temperatures translocation goes on more slowly than at higher. Hence the great value of anthocyan, assuming Pick's description of its properties, consists in its power, by



virtue of its absorbent qualities, of pushing forward translocation during the closing hours of the day : in enabling the plant to get a greater part of its work done while it is day.

The most important of Pick's experiments consisted in the study of the starch of assimilation formed by *Ricinus* leaves, and parts of leaves, whilst living behind various screens. He placed, for four hours of the day, the lobes of a leaf of a *Ricinus* plant behind, respectively, 1, ruby glass, 2, orange-coloured glass, 3, watery solution of the sap of red beet-root; whilst the fourth was directly insolated during the time of the experiment. He obtained, omitting those in the case of the lobe behind the orange glass, the following results : The lobe directly insolated contained much starch in its spongy parenchyma but more in the palisade cells; that behind the red-sap solution contained much starch in the conducting spongy tissue and less in the palisade; whilst in that behind ruby glass the starch was almost entirely confined to the spongy parenchyma, only a trace being found in the palisade tissue.

Pick's interpretation of his experiments is, that the lobes behind the red screens had assimilated as well and translocated better than those exposed to white light; and therefore this augmented transport of carbohydrate is due to the light absorbed by the anthocyan.

Wortmann (28) criticises these conclusions very severely, bringing forward the following objections : 1, before these inferences can legitimately be drawn it should be ascertained whether the rays absorbed by the anthocyan can, outside the living cell, increase the activity of diastase, the agent of translocation. Positive evidence at present available shows that this is not so, Detmer having proved that light is without influence on fermentation; 2, the results of Pick's experiments may be explained in quite another way. Wortmann adopts Stahl's suggestion that the palisade parenchyma of a leaf is an adaptation to bright light, the spongy tissue to light of feeble intensity, and thus explains Pick's results : that in bright light the palisade parenchyma will assimilate most actively and starch will appear in its cells;

in feeble light the spongy will appear to advantage as the assimilating tissue, and the greater number of starch grains will then be formed in its cells.

Till Wortmann's objections are rebutted by experiment, Pick's conclusions, that red light, as such, facilitates the translocation of carbohydrate material—and this by increasing the activity of the diastatic ferment—cannot be accepted. Pick's experiments however have to be reckoned with in any attempt to discuss the question of the functions of anthocyan; and it is now to be shown how Stahl harmonises them with experiments of his own and gives to them a simple interpretation.

In an important paper which appeared last year in the *Buitenzorg Annals*, Stahl (29) discusses with considerable fulness this anthocyan question, and brings experimental evidence to show that some of Kerner's hypotheses are, in all probability, correct.

The main fact which he establishes is that members, rich in anthocyan, have peculiar thermal properties, and that these supply the key to the solution of the problem in hand.

Kny (30) had demonstrated that the temperature of the water in a vessel filled with red leaves rose higher than that of water in a similar vessel containing green leaves; and Stahl obtains similar results, using the expressed sap of red-leaved Begonias. By more delicate experiments he fully confirms this heat absorption of anthocyan. In some experiments he uses a delicate thermopyle whose spathulate electrodes can be buried to any required depth in the leaf tissue; in others he measures the rate at which a thin layer of coco-butter melts from the different colour areas of a given particoloured leaf. His sources of heat are, in some cases, a gas burner, in others, a Leslie cube by which dark heat only can be used. In all cases he finds, in red-spotted leaves, that the red areas become warmer than the non-red when the leaf is exposed to a source of light or dark-heat.

These results Stahl applies to the interpretation of various phenomena observed by Kerner and Pick. Thus,



in the case of the Alpine plants *Linum* and *Satureja* to which reference has been made, Stahl suggests that the red *Satureja* thrives because its anthocyan enables it to take the fullest advantage of the sun's rays. Owing to it, the leaf reaches a higher temperature than it otherwise would ; and, in consequence, its general metabolic processes, not merely those of carbohydrate translocation, are favoured. The flax plants wither because they lack the colouring matter which would enable them to take advantage of any favourable change of temperature. And he observes a fact which, it must be confessed, however, might be taken to have merely a pathological significance, that in flax grown at 1800 metres, after exposure to nights during which the temperature fell to 0°C., the leaves were full of starch. A real difficulty seems to object itself to this simple interpretation : to wit, that, as Stahl shows, tissues containing anthocyan not only become warm more quickly than the ordinary green parts, but that, when the source of heat is removed, they become cool more quickly ; and until it be shown that excessive radiation is not a source of danger to such plants as those growing in high altitudes, it must appear at all events possible that what the plant gains by heat absorption during the day it loses, by increased radiation, during the night. Stahl is careful to point out that much of the foregoing is speculative, and contents himself with the statement that, in any case, his view of an acceleration of general metabolic activity by the heat-absorbing anthocyan (erythrophyll) has pressing claims for consideration. Pick's results Stahl explains in a similar way. The anthocyan is of importance not because it brings the red rays to bear on the translocation process in particular, but because by its heat-absorbing properties it furthers "die Stoff- und Kraft-wechsel Prozesse" of the plant.

The occurrence of anthocyan in very many localities, as for example extrafloral nectaries, the secreting end-cells of glandular hairs and at the foot of many sap-containing hairs is noted by Stahl, who expressly contents himself with pointing out that possibly here the colouring matter may

be of the same general service to metabolism as in the cases already cited. Whether, in the case of extrafloral nectaries, the red may be regarded as a signal to ants, as Schimper (31) has suggested, requires further investigation.

Perhaps a fair picture of how anthocyan may act in such cases as those just mentioned may be sketched as follows. In organs of plants of high metabolic activity tannins are of frequent occurrence. Tannins readily give rise to the colour-bodies whose thermal properties are such as may be conceived to be useful to the plant. External conditions such as intense light and low temperature are sufficient to set up the slight modification in direction of the metabolism of the tannins resulting in the formation of the colour-bodies. The principle of selection leads us to assume that *therefore* the anthocyan is useful : whereas if we followed the principle of experiment a whole series of researches would be required to establish the final proposition : as, for example, what exactly is the normal course of metabolism, how far can external conditions modify it and how is the plant affected when, by appropriate means, we prevent the formation of the anthocyan? In short : the explanation of an adaptation may be brilliant but cannot be sound since it is based on only one of the two scientific methods, deduction and induction. Hence to complete the fair picture just sketched we must add that experiments, to render it probable that the general mode of action of anthocyan consists in increasing metabolism, are still to be made.

Stahl applies his discovery of the considerable heat absorption by anthocyan to the case of anemophilous flowers in which red is the strikingly predominant colour, so much so, indeed, that it has led MacLeod (32) to express a doubt as to whether colours are indeed special adaptations to insect fertilisation.

The wind-fertilised flowers in question are those of many dicotyledonous trees such as the poplar, ash, elm, alder and hazel, and of shrubby plants as *Rumex* and *Poterium*. In such plants, flowering during the uncertain



weather of early spring, the red-colouring matter of the style, by virtue of its heat-absorbing powers, may materially accelerate the growth of the pollen tube toward the ovary and thus minimise the danger to the pollen grain from exposure on an unprotected stigma. Similarly the red colour of various gymnospermous flowers may accelerate their opening.

The deep red colour assumed in Alpine regions by the flowering spikes of various grasses such as *Poa annua* may have a similar significance—Kerner suggests indeed that probably the anthocyan converts “light rays” to heat—. We know that a rapid opening of some grasses is brought about by a quick growth of the anther filaments and that this can be effected by placing the grass spike in the mouth. How far this suggestion, that the heat-absorbing anthocyan favours the opening of flowers at the most propitious season, is capable of application to other brightly coloured Alpine flowers must for the present be left undecided; but, as Stahl remarks, a following up of the question seems likely to bring many interesting facts to light.

Hitherto plants, of more or less temperate regions only, have been considered and we have seen that in these the anthocyan probably functions as an accessory to chlorophyll in the absorption of radiant energy. According to Kerner the energy absorbed is that of the light waves which are converted by the fluorescent colour substance into heat: according to Stahl the heat rays are directly absorbed. The energy so acquired is applied to the accomplishment of the plant's metabolism, especially of the translocatory processes.

We come next to consider the distribution and function of anthocyan in plants of tropical regions.

Stahl points out that anthocyan occurs frequently in shade plants of the tropics, chiefly in the under epidermis, or in the spongy parenchyma of the leaf. In the steaming jungle, where a high temperature uniformly obtains, Stahl sees little need for a means of increase of general metabolism, and consequently casts about to

find some fundamental plant process in need of assistance.

Such a process is transpiration. Experiments made with branches of beech and hazel, bearing, in the case of either plant, red and green leaves respectively, show that the transpiration of the red leaves is greater than that of the green, especially if the branch be not exposed to direct sun, or if it be kept in an atmosphere rich in aqueous vapour; which conditions, it is to be noted, are those imposed by their habitat on shade-loving tropical plants.

Other experiments made with branches bearing red-spotted leaves, *e.g.*, *Polygonum persicaria*, *Maranta Kerchoviana*, in which the cut stalks were placed in eosin solution, showed that the liquid travelled first to the red patches of the leaf, from which it is reasonably inferred that transpiration is greatest in those areas. These experiments are the starting-point for Stahl's most interesting speculations. He recalls Wiesner's (33) discovery that plants in a saturated atmosphere may continue to give off water of transpiration owing to the conversion of light rays by chlorophyll into heat, and a consequent increase in tension of the aqueous vapour of the inter-cellular spaces in the plant above that of the vapour outside. Stahl reasons that anthocyan as a heat absorber may act in a precisely similar way and supplementary to the chlorophyll. Now there is indeed some evidence to show that transpiration of plants within the tropics may, under certain conditions, be very low. Haberlandt (34), whilst in Java, made experiments which gave the remarkable result that transpiration of plants belonging to the middle Europe flora is about half as much in the tropics as it is in their native habitat. Stahl has criticised these experiments adversely. Burgerstein (35) and Wiesner have shown conclusively that Haberlandt's results give a most misleading picture of normal transpiration within the tropics, since he excluded direct sunlight from his plants. Into these matters, however, we need not enter here, since Haberlandt's experiments, *under the conditions of his research*, are undoubtedly



trustworthy. They show that, in diffuse light and in a fairly saturated atmosphere, transpiration even in the high temperature of the tropics may be very low. Now these are the conditions to which the shade-plants are subject, and consequently Stahl's theory, that the anthocyan occurring in the leaves of such plants is of importance in the service of transpiration, seems tenable.

So much for the physiological side of Stahl's research. It remains only to refer to experiments which he conducted with a view to ascertain if any of the bright hues, characteristic of tropical foliage, can be regarded as warning colours. Since the bright colours of many flowers and fruits act as decoys to insects and to birds, it seems *a priori* possible that some of those of leaves may be of the nature of warnings to ward off attack.

Otto Kuntze (36) had, for instance, made the statement that the Javanese plant hedges of a red-leaved plant to warn away wild pigs. Stahl's inquiries, however, led him to conclude that the Javanese choose the colour to please themselves.

The result of experiments on feeding various animals, rabbits, sheep and goats on green and red leaves was that the red does not, to any noteworthy extent, act as a warning colour. In some cases the animals in question certainly preferred the green leaves when quite similar in other respects to the red ; but their prejudice gave way immediately when the red leaves were more tender or in other ways more desirable.

To briefly summarise Stahl's work. There is no good evidence for the screen-theory nor for that of warning leaf-colours. Anthocyan is of importance by virtue of its heat-absorbing properties. In temperate regions the heat so absorbed facilitates translocation and general metabolism, to the shade plants of the tropics it is an assistant to transpiration.

A paper endeavouring to arrive at wide generalisations by examining many of the scattered phenomena of colour to be met with in plants and animals has recently been written by Simroth (37). This author believes that all pigments

occurring in organic nature, both in their genesis and in their physiological, possibly indeed in their physical, significance, arise from a single cause, and go back to a single substance which is amalgamated with the original protoplasm and which in its further development and differentiation follows the simple spectral colours in the order of the rainbow. These be brave 'orts, but the author supports them, at all events to some extent, by many curious observations on colour phenomena, which he arranges, for his purpose, in three categories. First, he considers the psychophysiological evidence of vision. He states that with increasing decomposition of rhodopsin (visual purple) a series of colours is produced, running back to the primitive colour. Second, in a similar sense, he remarks the frequent change of colour in animals removed from shallow to deep water. Certain worms (*strudelwurmer*) have black-brown eyes in the former, whilst at great depths of the sea the colour is red (38). So, too, the algæ (*Florideae*) growing at the greatest sea-depths are red. A similar change to red is to be met with in animals and plants at high altitudes. These Simroth interprets, not as phenomena of adaptation, but of reversion. Third, the more complicated colour phenomena are most marked in animals, whereas in plants, whose metabolism is less active, the simpler spectral colours predominate. In plants too a change from yellow to green, from xanthophyll to chlorophyll is consequent on augmented metabolism; a change in the opposite sense marking a falling off of metabolism.

Even here Simroth does not reach the end of his speculative tether. He suggests that the cause of the nature of the primary pigment was either that in the earliest times the atmosphere was more watery and denser and thus let only the red rays through, or that protoplasm could at first only respond to the longer wave-lengths.

For botanists, the chief interest of this paper, the confirmation of the main points of which would naturally require far stronger and more exhaustive evidence than is vouchsafed, lies in the suggestion that in cases where no



adaptive significance can be established we have to do with a reversion to "primitive red".

The net result, to which an inquiry such as that recounted in this review leads, seems to be the exceedingly trite one summed up in the great surgeon's dictum, "Don't think, try!" that it is superlatively necessary in such biological problems as that proposed by this anthocyan to attack by actual experiment: that explanations as ready as they are rough, the formulation of which tends to become a pernicious habit, only obscure the true issues concerned.

Biology, in its modern sense, is the subtlest Physiology, dealing with refinements of fundamental processes, and must if it is to join in the procession of truth, follow in the wake of Physiology and "stand upon the order of its going".

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F. W. KEEBLE.

MEAN VALUES, FOR THE YEARS SPECIFIED, OF THE  
LOCATIONS ARE RECEIVED

Place.	Latitude.	Longitude.	Year.	Declination.
Pawlowsk - - -	59° 41' N.	30° 29' E.	1894	0° 10.5' E.
Katharinenburg - - -	56° 49' N.	60° 38' E.	1894	9° 39.4' E.
Kasan - - -	55° 47' N.	49° 8' E.	1892	7° 30.8' E.
Copenhagen - - -	55° 41' N.	12° 34' E.	1894	10° 41.3' W.
Stonyhurst - - -	53° 51' N.	2° 28' W.	1895	18° 37.8' W.
Hamburg - - -	53° 34' N.	10° 3' E.	1895	11° 42.7' W.
Wilhelmshaven - - -	53° 32' N.	8° 9' E.	1895	12° 52.5' W.
Potsdam - - -	52° 23' N.	13° 4' E.	1895	10° 19.9' W.
Irkutsk - - -	52° 16' N.	104° 16' E.	1894	2° 8.0' E.
Utrecht - - -	52° 5' N.	5° 11' E.	1894	14° 21.1' W.
Kew - - -	51° 28' N.	0° 19' W.	1896	17° 10.8' W.
Greenwich - - -	51° 28' N.	0° 0'	1895	16° 57.4' W.
Uccle (Brussels) - - -	50° 48' N.	4° 20' E.	1893	14° 48.7' W.
Falmouth - - -	50° 9' N.	5° 5' W.	1895	18° 54.5' W.
Prague - - -	50° 5' N.	14° 25' E.	1895	9° 31.5' W.
Parc St. Maur (Paris)	48° 49' N.	2° 29' E.	1894	15° 15.2' W.
Vienna - - -	48° 15' N.	16° 21' E.	1894	8° 43.6' W.
O'Gyalla (near Buda Pesth) - - -	—	—	1894	7° 58.2' W.
Pola (on Adriatic) - - -	44° 52' N.	13° 51' E.	1895	9° 47.0' W.
Nice - - -	43° 43' N.	7° 16' E.	1893	12° 32.7' W.
Toronto - - -	43° 40' N.	79° 30' W.	1895	4° 45.3' W.
Perpignan - - -	42° 42' N.	2° 53' E.	1894	14° 5.7' W.
Rome - - -	41° 54' N.	12° 27' E.	1891	10° 45.1' W.
Tiflis - - -	41° 43' N.	44° 48' E.	1894	1° 43.1' E.
Madrid - - -	40° 25' N.	3° 40' W.	1895	16° 6.6' W.
Coimbra - - -	40° 12' N.	8° 25' W.	1895	17° 42.0' W.
Washington <sup>1</sup> - - -	38° 55' N.	77° 4' W.	1894	3° 39.9' W.
Lisbon - - -	38° 43' N.	9° 9' W.	1895	17° 39.1' W.
Zi-ka-wei - - -	31° 12' N.	121° 26' E.	1894	2° 16.5' W.
Hong-Kong - - -	22° 18' N.	114° 10' E.	1895	0° 27.8' E.
Colaba - - -	18° 54' N.	72° 49' E.	1895	0° 36.9' E.
Manila - - -	14° 35' N.	127° 11' E.	1895	0° 51.6' E.
Batavia - - -	6° 11' S.	106° 49' E.	1894	1° 27.6' E.
Mauritius - - -	20° 6' S.	57° 33' E.	1894	9° 59.4' W.
Melbourne - - -	37° 50' S.	144° 58' E.	1894	8° 13.6' E.

<sup>1</sup> At new observatory, situated some little distance from old station.



## MAGNETIC ELEMENTS AT OBSERVATORIES WHOSE PUBLISHED AT KEW OBSERVATORY.

Place.	Year.	Inclination.	Horizontal Force, C.G.S. Units.	Vertical Force, C.G.S. Units.
Pawlofsk - - -	1894	70° 43·6' N.	·16456	·47061
Katharinenburg - - -	1894	70° 40·0' N.	·17799	·50729
Kasan - - -	1892	68° 36·2' N.	·18551	·47345
Copenhagen - - -	1894	—	·17373	—
Stonyhurst - - -	1895	68° 59·2' N.	·17148	·44637
Hamburg - - -	1895	67° 44·3' N.	·18009	·43994
Wilhelmshaven - - -	1895	67° 54·5' N.	·17983	·44305
Potsdam - - -	1895	66° 39·8' N.	·18720	·43392
Irkutsk - - -	1894	70° 10·5' N.	·20116	·55796
Utrecht <sup>1</sup> - - -	1894	67° 10·1' N.	·18416	·43737
Kew - - -	1896	67° 22·3' N.	·18309	·43924
Greenwich <sup>2</sup> - - -	1895	{ 67° 15·9' N. 67° 14·9' N. }	·18323	{ ·43727 ·43692 }
Uccle - - -	1893	66° 28·4' N.	·1877	·4311
Falmouth - - -	1895	67° 0·4' N.	·18547	·43708
Prague - - -	1895	—	·19834	—
Parc St. Maur - - -	1894	65° 5·2' N.	·19631	·42264
Vienna - - -	1894	63° 12·1' N.	·20740	·41061
O'Gyalla - - -	1894	—	·21054	—
Pola - - -	1895	60° 34·0' N.	·22026	·39038
Nice - - -	1893	60° 26·4' N.	·22198	·39139
Toronto - - -	1895	74° 34·3' N.	·16645	·60313
Perpignan - - -	1894	60° 10·4' N.	·22326	·38943
Rome - - -	1891	58° 4·6' N.	·2324	·3730
Tiflis - - -	1894	55° 46·9' N.	·25680	·37761
Coimbra - - -	1895	59° 43·6' N.	·22581	·38685
Washington - - -	1894	70° 34·3' N.	·19979	·56646
Lisbon <sup>3</sup> - - -	1895	58° 15·7' N.	·23344	·37731
Zi-ka-wei - - -	1894	46° 0·7' N.	·32613	·33785
Hong-Kong - - -	1895	31° 46·6' N.	·36480	·22589
Colaba - - -	1895	20° 48·5' N.	·37444	·14230
Manila - - -	1895	16° 49·0' N.	·37808	·11426
Batavia - - -	1894	29° 13·7' S.	·36749	·20563
Mauritius - - -	1894	54° 41·6' S.	·23958	·33829
Melbourne - - -	1894	67° 16·9' S.	·23426	·55956

<sup>1</sup> The Inclination and Vertical Force are from eye observations at 2 P.M.<sup>2</sup> Of the two values of the Inclination and Vertical Force, the first is based on observations with 3-inch dip needles only, the second on combined observations with needles of 3, 6, and 9 inches.<sup>3</sup> New dip needles.

## THE POSITION OF SPONGES IN THE ANIMAL KINGDOM.

THERE is no group of animals whose affinities and systematic position have been, from the earliest times to the present day, so much a matter of dispute and uncertainty as in the case of sponges; scarcely any theory can be imagined, possible or impossible, which has not been put forward at some time or other. It will be the object of this paper, not indeed to attempt to add another theory to those already existing, but to discuss the problem of the true nature of sponges in the light of the most recent researches upon the group, in the hope of being able to arrive at a decision in favour of one or the other of the many opposing views. An inquiry of this kind falls naturally into three parts: first, an exposition of the various opinions that have been put forth; secondly, a brief critical discussion of the leading features of sponge organisation and development which are of importance for the question at issue; and, finally, any conclusions which may be drawn from the facts in favour of one or the other theory.

Even as late as the middle of this century, the realm of nature to which sponges belonged, whether animal or vegetable, was still a matter of discussion. We need not, however, trouble ourselves with this controversy, long since laid to rest, but we will concern ourselves only with those theories which assign to sponges some place or other in the animal kingdom; and it will be convenient, in considering the different views that have been expressed, to classify them in order according to the systematic position which they assign to the group. We have then three main classes of theories, each with several subdivisions, according as their authors group sponges (1) as Protozoa, (2) as a distinct phylum descended from the Protozoa but distinct from the Metazoa, and (3) as Metazoa.



## I.—THE SPONGES AS PROTOZOA.

The older observers, whose histological technique consisted for the most part of tearing up bits of living sponges with needles, and examining preparations made in this way with microscopes which we should not now consider very first rate, nearly all considered sponges as Protozoa. In their preparations they always saw amœboid cells, which could be observed to move about, and sometimes they saw flagellated cells as well. Hence sponges were regarded as colonial forms of Rhizopods, or as masses of Infusorians, intermediate between amœbæ and monads. The former view, advocated by Perty (1852, p. 185), was advanced by Carter (1848, p. 310), who says of the fresh-water sponges: "The animals of which they are but a congeries are identical with the infusorium *Proteus*". The second view, put forward by Dujardin (1841, p. 306), is the opinion towards which Lieberkühn (1856, p. 512) was more inclined. Saville Kent (1870, p. 217) also regarded the sponge body as "an aggregation of amœbiform animals, building up amongst themselves a common skeletal support," and considers sponges, "in a natural and morphological system of classification, to be ranked as the highest representatives of the Protozoa".

The theory of the Protozoan nature of sponges took an entirely new turn with the discovery by James-Clark (1867) of the collar cells of sponges and their great similarity, amounting almost to identity, with the peculiar class of flagellate Infusorians, named by Saville Kent Choanoflagellata. James-Clark (p. 324) declared the sponges to be simply colonies of Choanoflagellata, and expressed the opinion that the collar cells of the different genera of sponges would be found to resemble the various genera of the collared monads, so that it would be possible to divide the genera of sponges amongst the families of the Choanoflagellata.

Both Carter and Saville Kent were converted to this view, and it may be said that the appearance of James-Clark's memoirs was practically the end of all discussion

as to the Rhizopod affinities of sponges. Carter, however, combined an acquiescence in James-Clark's theory of the Choanoflagellate affinities of sponges with peculiar views of his own as to the relationship of sponges to compound Ascidians. He invented the term "spongozoon" or sponge animal for the collar cell, and in 1872 he says (p. 47): "The spongozoon . . . is *the* animal which constructs the sponges generally". In 1874, discussing the flagellated chambers, or ampullaceous sacs as he termed them, he places under this head-line the query (p. 436), "Haeckel's 'gastrula' when developed *in situ*?" He goes on to remark (p. 438): "At one stage the young Ascidian is almost identical in appearance with the ampullaceous sac, that is, composed of a pavement of cells aggregated into a sac-like form. . . . The development of the ampullaceous sac is arrested, and the cells adapt themselves to that condition which ends in the evolution of a sponge; while the sac and its cells in the development of an Ascidian grow to the evolution of a compound tunicated group." After a comparison of the human ovum and a Protozoon he says: "Hence we see that an organic cell may be at one time one thing, and at another another, arising simply from adaptation to the functions required. Thus the cell or spongozoon of the ampullaceous sac becomes an individualised animal, and the *whole* sac, with its oral and anal apertures, so far like an Ascidian; while the sac with its pavement-lining of cells in the compound tunicated animal, goes on unarrested to produce an Ascidian." And he adds: "To produce the 'adaptation' there must be, of course, a creative or directing power, which being *infinite*, we can never comprehend".

Kent in his *Manual of the Infusoria* (1881, vol. i.) devoted a chapter to the affinities of sponges and argues strongly for classifying them with the Flagellata amongst the Protozoa. Besides the great resemblance of the collar cells to the Choanoflagellata he brings forward other grounds in support of his argument, some of which have not been confirmed, while others have been found erroneous by subsequent observers. His most valuable



contribution to the subject was undoubtedly the discovery of a peculiar form of colonial Choanoflagellates, to which he gave the name *Protospongia*, afterwards corrected by him in his description of the plates to *Proterospongia*, the former name being preoccupied. The interest of this form lies in the fact that it consists for the most part of a structureless jelly in which zooids of different kinds are imbedded; at the exterior are typical Choanoflagellate zooids, which serve for the nutrition and locomotion of the colony; in the interior are found amœboid zooids, which arise by modification and immigration of the Choanoflagellate zooids, and which multiply by binary fission dividing up to form spore masses. Each spore becomes a "simple minute unflagellate monad" which travels to the surface of the colony and is set free. There is thus formed in the interior of *Proterospongia* a tissue very like the gelatinous parenchyma of sponges, especially of those without a skeleton.

From *Proterospongia* it is easy to understand Kent's idea of the nature of sponges. He regards, in fact, a sponge as consisting also of collar-bearing monads, imbedded in a jelly containing amœboid cells, the latter derived by modification of the collar cells. Those amœboid cells may secrete a skeleton, which is, however, not essential. As in *Proterospongia*, so in sponges, Kent professed to have discovered a sporular method of reproduction of the zooids.

Collar cells according to him (p. 174) retract their flagella and collars, "assume a quiescent or encysted state," and "become resolved into the spore masses". "The sponge body is, by ever-progressing internal spore production, rapidly increased in size" (p. 176). These statements of Kent are not supported by the testimony of any other observer, and it is extremely probable, as Schulze remarks (1885, p. 186), that Kent has mistaken bodies of various kinds, such as spermatozoa, pigment granules, cells containing reserve material, etc., for spore masses. Kent denies the existence of spermatozoa and sexual reproduction altogether in sponges. The supposed ova, according to him (p. 187), are simply retromorphosed collar cells, which

“through coalescence with their fellows attain by degrees the comparatively colossal proportions they present” and then by segmentation produce the larva. The latter he considers not to be a larva in the sense in which the word is used among the Metazoa, but “a motile swarm-gemmule, consisting of a more or less ovate colonial aggregation of typical collared zooids” (p. 183). We shall return later to the question of the larva and its composition. Suffice it for the present to say that Kent draws the conclusion (p. 193) that though sponges form in many ways a transitional group between Protozoa and Metazoa, they nevertheless remain Protozoa in every detail, their position being inseparable from the Choanoflagellata, which in their turn lead back to the simplest flagellate monads.

## II.—THE SPONGES NEITHER PROTOZOA NOR METAZOA.

If animals composed, as are sponges, of several kinds of tissues, made up of structurally differentiated cells adapted to various functions, are to be classed as Protozoa on the ground that certain of the cells have a great resemblance to certain forms of Protozoa, then the term loses all meaning and becomes impossible to define. We might as well regard man as a Protozoan colony, on the ground that his leucocytes resemble amœbæ. But that sponges are not Protozoa is no reason for classing them as Metazoa, at least if we use the term Metazoa in a genetic, and not merely a descriptive sense, and mean thereby a group or sub-kingdom descended doubtless from the Protozoa, but through a common ancestor which had advanced beyond the stage of a Protozoan colony. This, the usual conception of the term, renders quite intelligible the idea of the existence of other phyla, which like Metazoa are descended from Protozoa, but along independent lines of descent. Thus some authors who have been unable to entertain the notion that sponges were to be classified as Protozoa, have nevertheless been equally unable to regard them as belonging to the Metazoa.

Bütschli (1883, p. 424) was the first to advocate such an idea, and says: “I am of opinion that the group of sponges is one quite shut off from other Metazoa, which arose quite



independently from the class Choanoflagellata". Sollas, though formerly of a different opinion, came round to the same view and proposed (1888, xcii.-xcv.) the name Parazoa for sponges, as a name of the same genetic and systematic value as Metazoa. He regards the possession of collar cells, as well as certain developmental facts, as distinguishing them from the Cœlenterata, the most primitive Metazoa, which in their turn are distinguished by the possession of nematocysts.

Finally Delage (1892, p. 416) has come to the conclusion on developmental grounds, that "the sponges show a progressive differentiation of their elements; but this differentiation does not take place from the beginning in the sense of germ layers comparable to those of other animals". He thinks they may be descended from Protozoa, "but that they have followed since the beginning an isolated development at the side of the stem of the Cœlenterates and other Metazoa".

### III.—THE SPONGES AS METAZOA.

The majority of authors, impressed by many facts of sponge organisation, such as their being composed of differentiated cells and tissues, their sexual reproduction, with ova and spermatozoa, and their development through a free swimming larva composed of distinct germinal layers, have regarded sponges as Metazoa, that is to say as descended from an ancestor which had passed the colonial protozoan stage, and which was common to them and other Metazoa. This does not mean however that the majority of authors are united in their opinions; far from it. We have next to distinguish two different points of view, those who regard sponges as cœlenterates, and those who consider them a phylum of Metazoa distinct from the cœlenterates. It is more convenient to take the latter first.

#### (a) *The Sponges Metazoa but not Cœlenterata.*

If sponges are not cœlenterates, the next question which arises is, are they composed of the same primary germ layers, ectoderm and endoderm, as are cœlenterates and all other Metazoa?

Vosmaer (1887, p. 481) while considering the sponges as Metazoa, but not cœlenterates, prefers to leave the question of the germ layers undecided.

Balfour thought that "the germinal layers of the sponges very probably do not correspond physiologically to the germinal layers of other types" (1885, vol. ii., p. 345) whether or not he regarded them as corresponding genetically, *i.e.* as homologous, is not very clear. The great contradictions which were presented by the facts of sponge development as then known, probably prevented him from expressing a definite opinion, for he hints that there are "strong arguments for regarding the Porifera as a phylum of the Metazoa derived independently from the Protozoa". In his discussion of the development of *Sycon* however (1879) he certainly seems to regard the two layers of the amphiblastula larva as corresponding to those of other Metazoa, but as becoming reversed in position at the metamorphosis, the "locomotor and respiratory" ciliated cells passing to the interior, the amœboid nutritive cells to the exterior.

Maas (1893) puts forward the view that sponges are derived from two layered Metazoan ancestors composed of ectoderm and endoderm, which have taken on a course of development diverging from all other Metazoa, in that the germ layers have become reversed in position, the true ectoderm being internal in the adult, and the true endoderm external.

Heider (1886, p. 230) considers sponges "true Metazoa, and the two primary layers of this group as really homologous with those of higher types," but they are to be separated from the cœlenterata, and regarded as an independent type. Only the blastula and gastrula stages in development are common to both (p. 233).

Goette (1886) also believes that "in the embryonic development of sponges we meet with the blastulæ and gastrulæ common to all Heteroplastids, as the modified ancestral forms of this group also" (p. 51). He thinks, however, that the apparent contradictions in sponge embryology can only be reconciled on the theory that the



ectoderm disappears, and the entire sponge is built up of endoderm, as he claims to have observed in the development of *Spongilla*. On the other hand, "the cœlenterate nature of sponges or their close relationship with the Cnidaria is not in any way supported by their developmental history".

This theory has been further supported by Goette's pupil, Nöldeke (1894), who comes to the following conclusions (p. 185):—

"(1) Sponges possess a typical gastrula with ectoderm and endoderm, which have the typical relations of position to one another.

"(2) The further development of the germ-layers of sponges does not correspond with that known as typical. The ectoderm undergoes a process of degeneration after fixation of the larva, in consequence of which it takes no share in building up the perfect animal.

"(3) Sponges have no genetic relationship with the rest of the Metazoa anywhere above the gastrula stage."

(b) *The Sponges as Cœlenterates.*

This is to a great extent the dominant view of sponge affinities; it is the view to be found in most text-books, and generally held by those who are not themselves experts on the question, a fact doubtless largely due to the great names that endorse this opinion. It must not be supposed, however, that here, any more than among the supporters of other theories, shall we find unity of opinion.

The view that sponges were true cœlenterates was first put forward definitely by Leuckart (1854, p. 472) in the following words: "If we imagine a polyp colony with imperfectly separated individuals, without tentacles, stomachal sac and internal septa, we have, in fact, the image of a sponge with its large 'water canals' opening outwardly".

It was, however, Haeckel who first brought this view into prominence. After his pupil, Miklucho-Maclay, had already (1868, pp. 236, 237) affirmed the common descent of sponges and cœlenterates, Haeckel in 1870 laid down the following thesis: "The sponges are most nearly allied to

the corals of all organisms. Certain sponges differ from certain corals only by a less degree of histological differentiation, and especially by the want of urticating organs. The most essential peculiarity of the organisation of sponges is their nutritive canal system, which is both homologous with, and analogous to, the so-called cœlenteric vascular system, or gastro-vascular apparatus of the Cœlenterata. In the sponges, just as in the corals, and indeed in the Cœlenterata generally, all the different parts of the body originate by differentiation from two primitive simple formative membranes or germ lamellæ, the entoderm and the ectoderm. These two lamellæ originate by differentiation from the originally homogeneous cells which (having been produced by the segmentation of the ovum) compose the spherical body of the ciliated embryo, or of the primitive larva (Planula). From the inner or vegetative germ-lamella, the entoderm, originate the nutritive epithelium of the canal system and the reproductive organs. From the outer or animal germ-lamella, the ectoderm, all the other parts originate" (p. 6). According to Haeckel the absence of nematocysts or urticating organs in sponges and their constant presence in corals, Hydromedusæ, and Ctenophora, is the sole morphological character separating the first class from the last three (p. 7). The mark of a sponge individual is the osculum (p. 8), representing the Cœlenterate mouth. The inhalant pores of sponges find their homologue in the cutaneous pores of corals. "Sponges and corals," he concludes (p. 13), "are near blood relations." From the common ancestor of both, the *Protascus*, originated as two branchlets the *Prosycum*, ancestor of sponges, and the *Procorallum*, ancestor of corals.

These statements of Haeckel's were the cause of a controversy between Kent and Lankester, the former maintaining the Protozoan affinities of sponges, the latter defending Haeckel. "Admitting," says Kent (1870, p. 204), "that . . . there in all probability did exist a something equivalent to Haeckel's hypothetical *Protascus*, and from which the existing stock of sponges and corals has probably been evolved . . . the evidence he brings forward in support of the proposed



intimate relationship of the two groups, as they *now* exist is based rather on affinities of analogy than homology." In reply to this admission, which drew from Haeckel the retort that Kent did not so much as know the difference between homology and analogy, Lankester (1870) pointed out that if the structures common to the two groups be derived by descent from a common ancestor they are homologous. To this Kent made the somewhat weak rejoinder (1870, p. 251) that the admission of Haeckel's *Protascus* was "meant to carry with it the vaguest possible significance and simply as an acknowledgment of my faith in the doctrine of evolution," and states his belief that "the open sac-like contour of all existing coelenterates and a few exceptional spongiadæ has probably been arrived at by two very different processes of evolution". Kent further sought to contrast the manner in which sponges secure food by ciliary action, as "a purely mechanical and involuntary force" with the voluntary muscular force exerted by an Actinian in seizing its prey (p. 208), a comparison which, as Lankester remarked, proposes to distinguish the two groups "by psychical manifestations" (p. 87). Lankester points out that in Kent's manner of "viewing" sponges all organisms might be classed as Protozoa, and concludes that the result of Haeckel's arguments will be to cause naturalists to admit the separation of sponges from Protozoa, but that "he will have greater difficulty in getting the association with Coelenterata, and with Anthozoa in particular, admitted".

In 1872 Eimer published a paper describing thread cells in sponges. Carter (1872) at once pointed out, however, that these thread cells did not belong to the sponge but to symbiotic hydroids living in the sponge tissue, and nematocysts have not since then figured in sponge literature. Haeckel, however, in his monograph of the calcareous sponges, published in the same year, modifies his view of sponge affinities. It is now the hydroids and not the corals with which he tries to compare sponges. He regards the most primitive sponges as related to the most primitive Acalephæ, but "Sponges and Acalephæ are two diverging branches of the Zoophyte stem which have

developed from the common ancestral stem of the Protascus" (1872, vol. i., p. 461). In other words, it is no longer suggested that sponges are a group of the same systematic value as one of the divisions of the cœlenterates, but that they are equivalent in the system to all remaining classes of cœlenterates put together. Since Eimer had found nematocysts in sponges their possession is no longer to be regarded as characteristic of cœlenterates, but a distinctive feature of the two groups is the formation of pores in sponges, since he now admits that the cutaneous pores of acalephs are analogous and not homologous with those of sponges; as Kent had already declared to be the case.

Finally, in 1889 (p. 90), Haeckel came to regard the flagellated chamber as the primitive individual in sponges, "homologous with a Gastræa on the one hand and with a simple Hydroid on the other," and concludes: "The position of sponges in the animal kingdom as a separate phylum of the Cœlenterata . . . seems to be the most natural".

The change of position with regard to the cœlenterate theory of sponges which we see in comparing Haeckel's earlier and later writings, finds a parallel in the different stand-points taken by the authors who also support this theory. Marshall alone takes an extreme view similar to that in Haeckel's earlier works, and considers (1885) sponges true cœlenterates descended from a protactinia with tentacles and a radiate gastrovascular apparatus, which persists as the canal system. All other advocates of the cœlenterate nature of sponges take rather the view which may be said to dominate in the text-book and the lecture room, that the Cœlenterata are to be divided into two distinct and opposed groups, the Porifera or sponges, and the Cnidaria or polyps and medusæ. Schulze, whose opinion carries more weight than that of any other authority, after remarking on the similarity of sponge and cœlenterate larvæ, points out that the metamorphosis indicates the point at which a separation took place in phylogeny, but finds it difficult to determine what degree of organisation was reached before the separation took place. He considers, however, that there is very little to sup-



port Marshall's views, and thinks it probable that the oldest sponges had no radial diverticula of their central cavity but a simple sac-like form, like an Olynthus among the Ascons (1885, p. 191).<sup>1</sup>

I have left to the last the peculiar view expressed by von Lendenfeld, since it cannot be assigned a place in the classification of the sponge theories which I have adopted. In his *Monograph of the Horny Sponges* (1889) he compares sponges as "Mesodermalia" with other cœlenterates or "Epithelaria". Facing p. 885 he gives a figure of a tree, representing the pedigree of sponges and other animals. From a massive stem labelled "Protista" comes off a thick branch on the right, labelled at its origin "Animalia," and a little higher up, but before it has divided, "Cœlentera". Just above where this latter name is affixed come off two branches, Epithelaria and Mesodermalia. So far everything seems quite clear, especially when we read on p. 887 that the sponges form "a separate phylum in the *grade* Cœlentera of the Metazoa". But on p. 886 we read that: "The sponges have probably been developed independently of other Metazoa from Protozoan ancestors, the nearest existing relations to which are the Choanoflagellata," and that "the mode of the phylogenetic development of sponges was similar to that of other Metazoa". In spite of this view, however, the author "does not see that there is any justification for the establishment of a special sub-kingdom for the sponges. They are evidently Metazoa and no doubt Cœlentera in the sense given above, namely, the *grade* Cœlentera as opposed to the *grade* Cœlomata" (p. 888). This method of reconciling statements apparently so contradictory as that on the one hand sponges are Cœlenterates, and on the other hand separately descended from the Choanoflagellata, implies a conception of the animal kingdom essentially different from that of all the other authors

<sup>1</sup> Chun, who discusses the question of sponge affinities from the standpoint of a specialist upon Cœlenterata, may be referred to as one who, taking a high rank as an authority upon a group of animals other than sponges, supports the theory of their cœlenterate nature. See Brown's *Klassen und Ordnungen d. T.*, Bd. ii., Abth. 2 (Cœlenterata), pp. 86-96.

whose views we have been discussing, though the theory of a separate choanoflagellate ancestry for a class of coelenterates reminds one strongly of Kent's admission of a Protascus ancestor for both corals and a class of Protozoa. Doubtless, however, this admission on the part of Lendenfeld was also meant to carry with it the vaguest possible significance and simply as an acknowledgment of his faith in the doctrine of evolution.

From the above exposition of the various theories that have been held as to the nature of sponges, it will be seen that it would be difficult to bring forward a new and original opinion on this subject. No one has yet sought to prove that sponges are degenerate molluscs, arthropods or worms, or that they are the progenitors of Vertebrates, and there is undoubtedly an opening for a physiologist to find the ancestor of sponges in the king crab. Also the theory of Goette that sponges are made up of endoderm alone, suggests a counter hypothesis that they are composed of ectoderm alone. When these two classes of speculations have been brought forward there will remain, so far as I can see, absolutely no new theory of sponge affinities to be propounded.

I propose now to discuss shortly the leading characteristics of sponges and the evidence they afford in favour of, or against, one or other of the above theories. Even if it be not possible at present to arrive at a conclusion as to the true nature of sponges, it may be at least possible to demolish and eliminate some of the numerous theories that have been put forward, and so narrow the field of inquiry. And at the outset it must be repeated that the Protozoan nature of sponges cannot now-a-days be seriously discussed. We have to consider whether sponges have, or have not, a common descent with the Metazoa, and if this question be answered in the affirmative, then whether and to what degree they are or are not coelenterates. Perhaps the most striking feature of sponges as compared with other animals, is to be found in their peculiar "collar cells". In the lowest sponges, the Ascons, the collar cells form a con-



tinuous layer lining the whole interior with the exception of a narrow rim round the opening of the osculum, where they are absent. In other sponges the collar cells form a discontinuous layer, being confined to certain parts of the canal system, the flagellated chambers. But however distributed they are never absent, at least not so in any sponge that has been properly examined. Not only are the collar cells a constant peculiarity of sponge structure, but they also occur nowhere else in the animal kingdom except in the case of the Choanoflagellata, where we meet with them as separate individuals leading a free existence, sometimes isolated, sometimes united to form colonies, but in no case losing their distinct individuality.

The agreement in form and appearance between the columnar collar cells with their long single flagellum surrounded by the delicate protoplasmic, retractile collar, and the individuals of the Choanoflagellata, is very striking. The variations in the size, form, and appearance of the collar cells in different sponges, are not greater than the variations found amongst the species of Choanoflagellata, if indeed they are as great. The physiological similarity seems to be on a par with the structural resemblance. It is certain that the collar cells take up food particles, and it is probable that this is effected in the same manner as in the case of the Choanoflagellata, namely, through the particles being swept by the flagellum into or upon the collar. Polejaeff (1883, p. 15) has tried to show that the collar cells are not fitted for capturing food particles on the ground that the lashing movements of the flagellum would tend to drive the particles away; but any one who has observed the action of the flagellum in the free Flagellates knows that it is exerted in a manner which would not have this effect. An *Euglena*, for instance, when swimming has its flagellum in front, and the body is dragged after it, as it were; if now an animal so moving were held fast by its tail and fixed in one spot, as are the Choanoflagellata and the collar cells of sponges, the consequence of the movements of the flagellum would be to direct a current of water towards the base of the flagellum, that is into the

cavity of the collar. In sponges in addition to the currents of this kind produced by each flagellum, there is the main current flowing through the canals and produced by the united action of all the flagella acting together. If this general current be considered alone in relation to the collar cells, it is evident that as it flows past the openings of the collars, each of the cup-shaped cavities which they contain forms a side eddy to the general current, and particles passing near the collars will tend to be carried into them and whirled about inside them by the eddy in their interior, until they come into contact with, and stick to, the protoplasm either of the collar itself, or of the cell at the base. Hence, taking into consideration both the effect of the collars in forming side eddies to the general current, and the manner in which the movements of the flagellum tend to sweep particles into the cavity of the collar, it is impossible to agree with Polejaeff that the collar cells are not suited for ingesting food; on the contrary they must be regarded as eminently well-fitted for a function which repeated experiments have shown them to exercise.<sup>1</sup>

While there is thus a close agreement between collar cells and Choanoflagellata in their general structure and functions, some details are still open to dispute. In the first place there is the question of contractile vacuoles; those authors who especially maintain the Protozoan nature of sponges, namely, Carter, Kent, and James-Clark, all assert the existence of pulsating vacuoles like those of Protozoa, and usually two in number, in the collar cell. These statements are not, however, confirmed by other authors, and though the protoplasm of the collar cells is undoubtedly very vacuolated in a number of instances, it is not certain that any of these vacuoles are contractile. Schulze (1885, p. 180) found the contractile vacuoles to be by no means so regular in their occurrence as usually alleged. Bidder (1895) makes no mention of them in his detailed account of the collar cells of Heterocœla. And the figure given of them by Kent in *Clathrina coriacea* (1881, pl. x., fig. 2) is certainly wrong, since he figures two

<sup>1</sup> Compare von Lendenfeld, *Zeitschr. f. wiss. Zool.*, xlvi., p. 674.



vacuoles at the base of the cell and the nucleus in the upper portion, but as a matter of fact in this species the nucleus is at the base of the cell and any vacuoles that occur are lodged in the upper portion. Hence the alleged occurrence of contractile vacuoles in collar cells requires further confirmation before such vacuoles can be regarded as constant features of the cells. A second point with reference to the collar cells is their multiplication. We have already noticed Kent's statement to the effect that they multiply by means of spores. He also asserts that the ciliated chambers develop from "the segmentation of a primitive amoeboid body produced . . . by the coalescence of more or fewer metamorphosed collared zooids". These assertions, so far as they have been noticed by subsequent observers, have generally been regarded as erroneous and without value. The fact remains, however, that both the multiplication of collar cells, and the formation of new ciliated chambers, in a growing sponge, are scarcely known, and no satisfactory observations have been recorded with reference to this point. Nevertheless the similarity of collar cells and Choanoflagellata remains a very striking fact, and furnishes the strongest argument, not only for those who seek to class sponges as Protozoa, but also for the authors who look upon them as descended from Protozoa independently of the Metazoa. Those, on the other hand, who regard sponges as Metazoa are obliged to explain the collar cells as secondarily acquired. Schulze (1885, p. 190) considers that the independent origin of collars in the cells of sponges is by no means impossible, since protoplasmic processes and membranes of various kind are of common occurrence in Protozoa. It would, however, have been more to the point to prove that similar structures occur among Metazoa.

While the collar cells have furnished the strongest argument for separating sponges from Metazoa, the peculiar canal system of sponges is a feature which, as may be seen from the opinions quoted above, has very often been used on the other side, especially by the advocates of the coelenterate theory. Not only was the central gastral cavity of

sponges regarded as an archenteron, lined by a true endoderm, but by the extreme coelenterists the osculum was homologised with the coelenterate mouth, and the system of inhalant and exhalant canals with the coelenterate gastro-vascular apparatus. It was soon established, however, that the sponge larva attached itself by what had to be considered, on the gastrula theory, as the blastopore, and hence the homology of osculum and mouth had to be given up.

It is not necessary to discuss further here the alleged homology of gastral cavity and stomach (archenteron), since it will be seen when we discuss the development that such a homology is now quite untenable. One side issue may however be noticed, since it is one that has contributed greatly to confuse the morphology of sponges. In a simple Ascon the internal cavity is lined by collar cells everywhere except at the oscular rim. On the theory that the gastral cavity represents the archenteron, we have in these simplest types the "endoderm" represented by a uniform layer of collar cells. In a Sycon, however, or any sponge above an Ascon, the collar cell layer is discontinuous and confined to the chambers, all the rest of the canal system being lined by flattened epithelium. But an archenteron cannot be imagined as lined by anything else but endoderm. Hence some part at least of the flattened epithelium lining the canal system had to be considered as endoderm, in spite of the fact that it could not be distinguished by any feature whatsoever from the flat "ectodermal" epithelium on the outer surface of the sponge. The exact limits of the "ectoderm" and "endoderm" in the interior of the canal system were much disputed, but the opinion expressed by Schulze (1880, p. 438) generally prevailed, according to which the endoderm furnished not only the collar cells of the chambers, but also the flat epithelium lining the excurrent system from the chambers to the oscular opening, while the ectoderm furnished the flat epithelium covering the outer surface of the sponge and all the incurrent canals up to the chamber pores. It followed therefore that an endoderm consisting primitively of a uniform layer of collar



cells became in part transformed into flat epithelium, and in Sycons, which start developmentally from an Ascon-like condition, this transformation must be continually occurring during growth. If, however, we examine the grounds other than theoretical upon which was founded this theory of the transformation, alleged to be of such frequent occurrence, of collared into flat epithelium, we find direct evidence of any kind, whether histological or embryological, to be entirely lacking. As is shown in the figures published by all trustworthy observers, and especially in those of Schulze, and as can be seen in any good preparations of sponge histology, the collar cells lining flagellated chambers or radial tubes always pass abruptly and without the slightest gradation into the flattened epithelium of the incurrent or excurrent canals. This was especially well shown by Schulze (1875) in his investigations upon just the very sponge in which direct evidence of the modification of collar cells into flattened cells might be expected to be forthcoming, namely, *Sycon raphanus*. Cells intermediate in form between the two kinds of epithelium do not occur, and the many figures of such transitions given by Lendenfeld must be characterised as erroneous. The fact, sufficiently obvious in itself, that a collar cell if cut obliquely may present in sections the appearance of a rounded or columnar cell without flagellum or collar, perhaps will account for some of these incorrect descriptions, though the considerable differences both in the structure of the nucleus and the nature of the cytoplasm between collar cells and flat epithelium cells ought to have been sufficient to prevent any such confusion.

Schulze was led by his observations upon *Sycon raphanus* (1875, p. 258) to regard the flat epithelium as a layer of uniform nature throughout, on account of its great similarity, amounting to identity, both at the outer surface of the body and in the interior of the canal system. His embryological investigations upon *Plakina* (1880) first led him to express the contrary view referred to above. It cannot, however, be said that his figures of the latter form afford any direct evidence of an "endodermal" flat

epithelium. A stage showing the internal cavity of the young sponge lined by columnar cells is compared with a later stage in which flagellated chambers open into a gastral cavity lined by flat epithelium. From the comparison it is inferred that the flat epithelium of the gastral cavity owes its origin to a flattening of the columnar "endoderm" cells. Two other inferences, however, are just as possible, either that the lining of flat epithelium originates by an exposure towards the gastral cavity of the outer germinal layer when the "endoderm" is aggregated into the chambers, or that the columnar cells of the earlier stage are not all "endoderm".<sup>1</sup> In any case *Plakina* is, like *Halisarca*, one of the forms which requires renewed investigation, the facts of its development as at present recorded standing in irreconcilable contrast with the development of other forms.

It must therefore be granted that, with all the respect deservedly due to so great an authority, Schulze has not brought forward absolutely convincing proof of the origin of the internal flattened epithelium by modification of the collared gastral layer. On the other hand such direct embryological evidence as exists with reference to the origin of the flat epithelium of the interior shows it to be derived from the *dermal* layer, the inner cell mass of the larva. Both Maas (1892 and 1893) and Delage (1892) are united upon this point, and agreed that the ciliated layer of the larva furnishes the chambers, and nothing else. To establish what may be termed *the continuity of the ciliated cells* is, as we shall see, the tendency of recent investigations upon sponge embryology; that is to say, the ciliated cells of the larva become the ciliated cells of the adult, in spite of the very great changes in position this implies, and nothing else is formed from them. In other words, the gastral layer when once differentiated remains uniform in nature throughout the life cycle.

Nothing is more difficult than to establish a negative, and the above conclusion as to the uniformity of the gastral layer would be at once upset if it were shown clearly and in a trustworthy manner that in any single case collar cells are

<sup>1</sup> Compare Maas (1893), pp. 423, 424.



transformed into flattened cells. For the present I think, however, we are justified in regarding the notion as one of the many assumptions which, founded on a mistaken theoretical basis, and opposed rather than supported by the facts, have dominated and falsified sponge morphology.

The physiology of sponges, so far as it is known, does not present much analogy with the Metazoa generally, or with coelenterates in particular. Although much is uncertain or unknown, three things are fairly established. First, that the osculum is always an exhalant opening, from which issue forth the currents which enter at the pores and stream along the canals. Secondly, that ingestion may be performed by either layer. Numerous experiments by Lieberkühn, Metschnikoff and others, have shown beyond all doubt the capacity of the collar cells to take up small food particles from the water which apparently they transfer to the amœboid cells. On the other hand Metschnikoff (1879) showed clearly that in some sponges (*Reniera*) the food particles are ingested by cells in the dermal layer, and his observations have been confirmed and extended by subsequent investigations.<sup>1</sup> Metschnikoff also confirmed the observation of Lieberkühn (1857, p. 388) to the effect that in *Spongilla*, Infusoria carried in by the current through the pores into the subdermal spaces and inhalant canals were absorbed there by the wandering cells; a fact which helps to explain the great development of the inhalant canal system in higher sponges, and throws light on the superior benefit derived by the sponge from the more complicated canal systems as compared with simpler forms such as the Ascons, which are probably capable only of ingesting microscopic particles by means of their collar cells. A third principle of sponge physiology is that all digestion is intracellular, and apparently performed by the wandering amœbocytes, the “cellules digestives pigmentées” of Topsent. So far, therefore, as conclusions can be drawn from the physiology,

<sup>1</sup> E.g., by Lendenfeld in *Aplysilla violacea* (über Coelenteralen der Südsee II., etc., *Zeitschr. f. wiss. Zool.* xxxviii., 1883, p. 252); but in his more recent work (*ib.*, xlvi., 1889, p. 674) he goes back upon his former opinion.

it presents us with a more primitive, less specialised condition than we find in the Metazoa *sensu strictiori*.

The reproduction of sponges on the other hand is of a distinctly Metazoan type, by means of true ova and spermatozoa. This is a fact which has been called in question at various times, but, without entering into a detailed discussion, it must be regarded as established now beyond the possibility of doubt, in view of the accurate observations of Schulze upon various types of sponges, Fiedler (1888) upon *Spongilla*, and many other authors. Their evidence is in no whit invalidated by the fact that many of the descriptions of supposed spermatozoa relate in all probability merely to ordinary flagellated cells. On the other hand, full and detailed accounts of the phenomena of the growth and maturation of the ovum in different types are much to be desired. The only such account existing is that given by Fiedler (1888) with reference to the ovum of *Spongilla*, which shows some remarkable deviations from the type usually considered as the normal for Metazoa. The polar bodies, for instance, do not originate by a karyokinetic division of the nucleus of the ovum, but are, as it were, budded off after disappearance of the nuclear membrane from the large spherical chromatin mass occupying the centre of the vesicular nucleus. They arise, therefore, by a process more akin to direct division, and a quite similar process, only differing in that the central chromatin mass divides into equal halves within the still present nuclear membrane, occurs at each division of the nucleus during the segmentation of the ovum. The absence of karyokinesis in processes where its occurrence is usually so constant is the more remarkable when it is seen that true and typical mitoses are found in the tissue cells and the spermatogenesis of *Spongilla*. Not only are more observations upon other forms much needed, but the details of the fertilisation of the ovum are quite unknown in any sponge and remain for description.

Some authors have regarded the ovum of sponges as an asexual reproductive body made up of a fusion of cells. We have noticed already Kent's statement that the ovum



is produced by a fusion of retromorphosed collar cells. Goette (1886) also believed the ovum of *Spongilla* to be multicellular in nature, but his descriptions have been shown very clearly by Fiedler to be erroneous. More recently, H. V. Wilson (1894, pp. 285-294 and 327-329) regards the reproductive body from which the larva arises as in some cases a gemmule produced by cell fusion, in other cases as a true ovum (*Tedanione*, pp. 341-343). That an essentially similar free-swimming embryo should be in one case a true larva produced from a fertilised ovum, and in another case "a bud embryo exhibiting ancestral traits," derived from an asexual gemmule, is a state of things which would require very convincing proof before it could be accepted. It seems, however, far more probable that Wilson's statements, and also, we may add, those of Kent, rest as Maas suggests (1896, p. 233) upon a mistaken interpretation of a process of oögenesis.

The last feature of sponge organisation which we need discuss, namely, their embryonic development, is perhaps the most important of all when considering the question of their affinities. The ontogeny alone enables us to decide how far the resemblances between the adult forms of sponges and other animals are due to a similar origin, or are secondarily and independently acquired; in other words, to distinguish between what is homologous and what is analogous. And just as the reproduction seems to be of a distinctly Metazoan type, so also may be said of the earlier developmental history. The segmentation of the ovum presents no special features and may be described as total and regular. It results typically in a blastula of the usual type, from which the diblastula, or two-layered embryonic condition, arises in different forms in a variety of ways, all of them, however, paralleled in other groups of Metazoa. In the lower Ascons, in *Halisarca*, and in *Plakina*, it is formed just as in many Hydroids, by an immigration of cells either at any point or from the posterior pole. A simple modification of the latter type leads to the amphiblastula larva, the only larval form at all specially characteristic of sponges where the cavity is too small to contain the immigrated

cells which therefore protrude posteriorly (Minchin, 1896). In *Oscarella* the two-layered condition is formed by a simple invagination. Finally in the highly specialised Cornacuspongiæ the segmentation results in a solid morula or sterroblastula, and the two embryonic layers are differentiated *in situ*. In whatever way the two layers arise, the result is a two-layered larva presenting in most cases striking resemblances to the cœlenterate planula. It consists of an external ciliated layer more or less completely surrounding an internal mass of amœboid, granular, non-ciliated cells. When food yolk is present in any quantity it is contained in the cells of the inner mass. Hence in this point as well as in their relative position and general characteristics, the outer and inner layers of the sponge larva are quite similar to the ectoderm and endoderm of Cœlenterata and other Metazoa.

So far the way is clear, and the facts are scarcely disputed, even by advocates of the most opposed views. It is the metamorphosis of the simple sponge larva, that is to say, the fate of its component layers, and the part they take in building up the adult sponge, which is the important question to decide.

Before proceeding, however, to discuss this question it is necessary to be clear as to the terminology we employ for the cell layers under consideration. The words ectoderm, mesoderm, and endoderm, have been universally employed in sponges, sometimes in a purely descriptive sense, but more often as implying a homology with the similarly named layers in cœlenterates. Not only is such a homology more than doubtful, but even in a descriptive sense the use of these terms is in the highest degree confusing and misleading. For in the larva the ciliated layer has been termed the ectoderm, and the inner mass the endoderm or endo-mesoderm, while in the adult the term ectoderm has been applied to the external, and more or less of the internal epithelium, the term endoderm to the rest of the internal epithelium, and the term mesoderm to all the tissue enclosed between the epithelia. It is, however, far from certain, and indeed highly improbable, that the similarly named layers



of the larva and adult correspond, and a terminology which implies any such correspondence is to be avoided. Both for these reasons, and on account of the homologies implied by the words "ectoderm," "mesoderm" and "endoderm," I have proposed to revive for the layers of the adult sponge the purely descriptive terms originally coined by Haeckel (1872, vol. i., p. 130), namely, the term "gastral layer" to denote the internal collared epithelium and the term "dermal layer," to denote the remaining tissues. Thus the gastral layer corresponds in *Ascons* to the whole of the "endoderm" of authors and in other sponges to a part of it; the dermal layer is the "exoderm" of Haeckel, the "ectoderm" with the "mesoderm," and sometimes part of the endoderm of other authors.

The larva, as we have seen, consists of an external ciliated layer and an inner cell mass. How do these layers correspond with the layers of the adult? Which of the two layers of the larva is "gastral" and which is "dermal"?

In a former number of this journal (1894) I discussed the question of the relation of the layers of the sponge larva to those of the adult at some length, especially with references to the works of Maas (1892 and 1893) and Delage (1892). I showed that the works of these two authors, differing much in respect to details, but agreeing on the points of fundamental importance, rendered it possible for the first time to treat the embryonic development of sponges generally from a uniform and reasonable stand-point. Both authors, in fact, agreed in affirming that, contrary to the usual belief, the ciliated layer of the larva of *Cornacuspongiæ* passed into the interior at the metamorphosis and became the gastral layer of the adult, that is to say, the collar cells of the chambers, while the inner mass of the larva gave rise to the remaining tissues of the sponge, namely, to the flat epithelium lining the exterior and the in-current and ex-current canals, and the whole of the so-called mesoderm, in other words to the dermal layer as here defined. Thus it became at last possible to reconcile the apparent contradictions resulting from a comparison between the well-known development of *Sycon* and that of other sponges. There remained however certain cases

where the development required re-examination in the light of these views, in order to determine whether a similar reversion of the layers, not hitherto suspected, did occur, or whether the recorded statements were correct. These cases were, besides *Oscarella* with its somewhat peculiar development, *Plakina*, *Halisarca*, and the Ascons.

Since my review of these questions in this journal, three works have been published upon sponge development, those of H. V. Wilson (1894), Nöldeke (1894), and myself (1896). To take the last first, I have shown that in the Ascons the layers become reversed in a manner similar to that described by Maas and Delage, and that it thus becomes possible to homologise the parenchymula and amphiblastula types of development, the internal non-ciliated cell mass of the former being homologous with the posterior non-ciliated cells of the latter, and giving rise in the same way to the dermal layer of the adult.

The observations of Wilson on the other hand, dealing with several species of Monaxonida are interpreted by him in an opposite sense to the views expressed by Delage and Maas after a study of the same class of objects. Wilson believes that the ciliated layer of the larva becomes the "ectoderm," that is to say the dermal layer of the adult, and derives the collar cells, the "endoderm," from the inner cell mass of the larva. He thus brings us back once more to the old views of sponge embryology, which sought in vain to construct a uniform type of sponge development from a chaos of contradictory and irreconcilable observations.

Not only must I confess myself biassed against Wilson's views on general grounds, that is to say, on account of the impossibility of homologising in any other way the amphiblastula and, I may add, parenchymula larva with other types; not only am I greatly inclined to regard Wilson's statements as less convincing than those of Maas and Delage; but I consider that Wilson's own recorded observations are not at all in harmony with his interpretations of them. Wilson has objected strongly to his figures being taken as evidence against his views, a somewhat curious position to take up if his figures profess to be accurate; we can



but criticise what he puts before us. I must therefore venture to point out that he has figured in the plainest manner the immigration of the ciliated cells, and the formation of the chambers from them. On plate xvi., figs. 26, 27 and 28, show in surface view the growth of the inner mass over the ciliated cells; in fig. 30 we see the ciliated cells heaped up at one pole and becoming internal; figs. 39, 40 and 41 of plate xvii. show groups of these cells forming chambers, though their cell outlines are not represented; and figs. 44, 45, 47 (plate xviii.) and 50, show later stages with chambers formed of cells with small nuclei, similar to the larval ciliated cells. On plate xvii., again, fig. 36 shows some of the ciliated cells not yet absorbed, others scattered through the interior, and even arranged to form chambers, and figs. 38 and 43 represent later stages in which the chambers are well shown to be formed from the small cells. Finally attention must be drawn to the most important stage figured on plate xxi., fig. 85, showing in a larva just fixed the commencing inversion of the layers. Knowing how easy it is to represent in drawings what one believes the preparations to show, it is remarkable to find in Wilson's figures so much evidence for a view opposed to that which he holds, and the fact is certainly a great testimony to the accuracy of the author's observations. Wilson does not always represent the disproportion in size between the nuclei of the two layers as distinctly as has been done by Maas and Delage, no doubt because the point never occurred to him as one of importance. While, therefore, Wilson's figures must be cited as a most valuable contribution to the theory—or rather the facts—of the inversion of the layers, it may further be pointed out that he admits in the text that the ciliated cells at least partially travel inwards. On p. 299 after pointing out that "all the columnar cells cannot be transformed into flat cells," he says that the appearances suggest "that the ectoderm [*i.e.*, ciliated] cells are migrating at this point into the interior of the larva," and again on p. 319 he admits that "some of the ectoderm cells of the larva migrate into the interior during the metamorphosis". On p. 375 he makes the confession: "My observations on

the actual transformations of the ciliated cells . . . into the flattened epidermis . . . are . . . meagre" (yes, indeed!), and again admits on the same page "the immigration into the interior of a part of the ciliated cells". For all these reasons it seems to me not only justifiable but even necessary to regard Wilson as a supporter, in spite of himself, of the view that the layers become reversed during the metamorphosis. Wilson's memoir seems, in fact, to have been born out of due season, so to speak; an anachronism, as Maas has well termed it. Commenced, and apparently for the most part written, at a time when the inversion of the layers was not for a moment suspected, when Metschnikoff's almost prophetic statements (1874) had been forgotten apparently even by their author, Wilson's work came forth in an epoch in which the stand-point which it represented had already been clearly shown to be impossible, and the views it put forth were antiquated before they were published.

Nöldeke (1894) on the other hand, sees the facts of sponge development in a very different light. In the larva of *Spongilla* he has described in a most convincing manner the way in which the ciliated layer becomes broken up and carried into the interior after fixation. But with regard to the ultimate fate of these ciliated cells, Nöldeke's views are original and peculiar. He believes with Delage that the amœboid cells of the inner mass capture the ciliated cells and engulf them, in a manner analogous to phagocytosis (see SCIENCE PROGRESS, May, 1894). But whereas Delage believes that the cells so captured are set free again to form the chambers, Nöldeke is of opinion that they are completely absorbed and digested by the phagocytic amœboid cells. In other words he agrees with Goette, whose views have been quoted above, to the extent of believing the external ciliated layer of the larva to be lost, though not thrown off, during the metamorphosis, so that the whole sponge is built up from the inner mass alone. In this mass epidermic cells, amœboid cells and formative cells (*Bildungszellen*) are to be distinguished. The chambers are stated to arise from the latter, either by division up of a single cell, or by a coming together of cells from different



parts. Nöldeke, like Goette bases his theory of the loss of of a whole germ layer in sponges entirely on observations upon the development of *Spongilla*. How cautious we should be, however, in drawing any far-reaching conclusions from this apparently highly modified type is obvious from the fact alone that its development has been investigated by Ganin, Goette, Maas, Delage and Nöldeke, and that the observations of all these authors contradict each other upon even most essential points. Indeed, there is hardly any statement, even of detail, which is borne out by the testimony of a majority of the witnesses. I refrain on that account from a detailed criticism of Nöldeke's descriptions and figures, though a close examination might perhaps yield, as in the case of Wilson, results not quite in harmony with the author's conclusions. I will only say that while on the one hand the author's observations as to the immigration of the ciliated cells at the metamorphosis are most valuable and highly to be welcomed, on the other hand the theory of the complete absorption of these cells requires far more convincing proof, both for *Spongilla* and in the case of other types, before it can be entertained.

Goette, whom Nöldeke follows, attempted to give his theory of the loss of the "ectoderm" in sponge larvæ a wider basis of fact by interpreting in this sense the observations of Metschnikoff upon Calcareous Sponges—*Sycandra* and *Ascetta* (*Clathrina*). As regards *Sycandra*, few will, I think, deny that Schulze's well-known investigations render such an interpretation impossible. This conclusion is further borne out by my own observations on the amphiblastula of *Leucosolenia*, where I was able to trace the origin of the collar cells from the ciliated cells of the larva. In the case of other Ascons also I must give a most decided denial to the supposition that the ciliated cell layer is lost in development.

It may be said, therefore, that the embryological investigations upon sponges published since my review in the pages of SCIENCE PROGRESS, to which reference has already been made, tend on the whole to strengthen greatly views there advocated; namely, that a complete reversion of the layers takes place in the metamorphosis, whereby the ciliated

external layer of the larva becomes the internally placed collared epithelium of the adult, while from the inner mass of the larva arise the remaining tissues of the sponge body. There still remain two important cases where statements to the opposite effect remain on record uncontradicted, namely, the cases of *Halisarca* and *Plakina*. In view, however, of the great similarity of their larvæ to those of the lower Ascons it is difficult to believe their development to be of so fundamentally different a type as the recorded observations would force one to suppose. In the present condition of our knowledge it seems to me, that wherever statements exist to the effect that the inner and outer layers of the larva pass respectively into the inner and outer layers of the adult, we are justified in regarding such statements as false until they are proved to be true, instead of believing them to be true until they are proved to be false.

In order to complete and conclude our review of the main features of sponge embryology, there remains one small but important point for discussion; namely, Do the collar cells so characteristic of the adult ever occur in the larva? The point is one which has been thought to be of considerable importance as bearing upon the question of the affinities of sponges with Choanoflagellata. Kent, who as we know was a firm believer in a close relationship between the two groups, described collar cells with large and distinct collars as occurring in numerous larvæ, and tried to prove that the sponge larva was nothing more than a "colonial aggregation of typical collared zooids" (1881, p. 183). He also quoted Barrois (1876, pl. xv., fig. 29) as having figured similar collar cells in sponge larvæ.

Schulze (1885) on the other hand set himself to disprove Kent's statements, while arguing (p. 189) that on the theory of a descent of sponges from Choanoflagellata it might be expected that collar cells would make their appearance in that phase of sponge development which corresponds to a Protozoan colony in phylogeny, namely, in the blastula stage. Schulze, however, searched in vain for collars to the ciliated cells of *Sycandra*, and declares himself convinced (p. 182) that Kent's figures of "swarm-



gemmules" represent simply portions of the collar cell layer set free. Few, I think, will dispute the correctness of this interpretation, and it is easy to confirm Schulze's statement that such appearances can be readily obtained by teasing up living sponges, when also true larvæ may be set free with plates of collared epithelium sticking to the posterior pole, as figured by Kent (pl. ix., fig. 26). Schulze further interprets the hyaline and refractile margin figured by Barrois in the ciliated cells of *Oscarella lobularis*, not as a collar, but as the solid non-granulated terminal portion of the cell.

Shortly after Schulze's very thorough refutation of Kent's statements, Heider (1886), in his studies upon the development of *Oscarella lobularis* resuscitated the collars already described in the ciliated cells of the larva of this form. He found that each flagellum arose from a cup-shaped depression of the hyaline margin of the cell, and regarded this as the rudiment of a collar. The appearances figured by Barrois as the "collier des cellules" were explained as the rudimentary collar together with the hyaline cell margin. But he considered the occurrence of collar cells in sponge blastulæ as of no phyletic significance.

Heider's description of the structure of the ciliated cells of the *Oscarella* is very clear and convincing, but at the same time it is an open question whether such a shallow depression can really be regarded as a true collar. In any case I am unable to agree with him that the occurrence of collar cells in the blastula would be of no phyletic significance. At the same time I find myself unable to endorse Schulze's opinion, that the theory of descent from the Choanoflagellata should have as a necessary consequence the occurrence of choanocytes in the larva. For though the blastula no doubt represents a protozoan colony in phylogeny, it only represents it morphologically, and not physiologically; that is to say, the cells are not functionally active, except as regards locomotion, since they do not take in food, or at least have never been observed to do so. The collar, however, is always a sign of functional, and especially nutritive activity, most developed when the sponge is most expanded, and always to be found more

or less retracted, often completely so, when the sponge is contracted and closed up. Hence, for my part, I should not expect to find the ciliated cells of the larva provided with collars, even if it were quite certain that the theory of choanoflagellate descent were the true one. But on the theory of the continuity of the ciliated cells, which we have already discussed, the ciliated cells of the larva pass directly into the collar cells of the adult and develop collars after the metamorphosis, when the sponge begins to feed and grow. Hence it follows that the ciliated cells of the larva do possess the power of developing collars, and might be regarded as potential collar cells, in which the function of nutrition is temporarily in abeyance, and as a result the collars are not protruded.

From the foregoing review of sponge characteristics we may pick out four points of primary importance in the discussion of their affinities :—

(1) The unfailing possession of collar cells, and their great resemblance to Choanoflagellata. This, as we have seen, is the feature which has been the mainstay of those who advocate the relationship of sponges to Choanoflagellata or their descent from them, while those who advocate a contrary view are obliged to minimise the resemblances, or declare them due to analogous adaptation.

(2) The reproduction by ova and spermatozoa. This, on the other hand, is a feature which has furnished support to those who regard sponges as Metazoa of some sort or other. In view, however, of the many analogous sexual processes known to occur amongst Protozoa and in plants, it is perhaps not safe to lay too great stress upon this point, especially as the details of the process seem to be of a type rather more primitive than in other Metazoa.

(3) The formation of two germ layers by processes not specially characteristic of sponges, and the possession of a larva very similar to the coelenterate planula. This is certainly the strongest argument for the Metazoan affinities of sponges, and has always been much employed by the supporters of this view, especially by the coelenterists. We have already quoted many of the arguments based on this



point ; they were well summed up by Schulze (1885, p. 191) when he asserted "that the difference between the free swimming ciliated larvæ of sponges on the one hand, and of Cnidaria on the other, is not more considerable than the difference among sponge larvæ themselves".

(4) The reversion of the layers at metamorphosis. This fact, now sufficiently well established, is quite subversive of the cœlenterate theory. It is only necessary to read the arguments of the cœlenterists to see at once how completely it undermines their position. The cœlenterate theory assumes as the type or "Grundform" of sponges a hollow sac-like or vase-like organism, with the body wall composed of two layers, ectoderm and endoderm, and derived from an embryo composed of the same two layers similarly orientated. If, however, we make our comparison start from the adult forms, then the larvæ of sponges are quite anomalous, in that they possess an *ectoderm* derived from the *macromeres*, and often completely surrounded by the endoderm. If, on the other hand, we lay stress on the resemblances between the larvæ any comparison of the adult sponge to a cœlenterate is out of the question.

When, however, we try to decide by means of this point whether sponges are or are not Metazoa, we do not get much help, since in either case the interpretation of the ancestral history presents much difficulty. If the larva, say of a simple Ascon, be regarded as strictly homologous with the very similar larva of a hydroid, it is very difficult to understand why in the one case the component layers should be reversed at fixation and in the other case not. If on the other hand we regard the Ascon parenchymula larva as a repetition in development of an ancestral stage similar to *Proterospongia*, a free-swimming volvox-like colony of Choanoflagellata in which certain zooids were continually migrating into the interior, it is by no means easy to form a clear idea of the steps by which such a form came to reverse its layers and place its collared cells in the interior. Hence the metamorphosis of the sponge larva cannot be regarded as affording conclusive arguments in favour of either the metazoan or the choanoflagellate affinities of sponges. In so far, however, as it indicates

the ciliated cells of the larva to be potentially collared cells, as pointed out above, the reversion of the layers is slightly in favour of the choanoflagellate theory.

It is very evident that we have at present but two theories to choose between; either to regard sponges, with Bütschli, Sollas, and Delage, as descended from choanoflagellate ancestors independently of the Metazoa; or to regard them with Maas and, apparently Balfour, as true Metazoa composed of the two primary germ layers, ectoderm and endoderm, which have become reversed in position in the adults. The choice between these two theories will depend upon which of two assumptions we find most difficult. If sponges are Metazoa, the collar cell, occurring in no other Metazoa, must have been independently acquired. If sponges are descended from Choanoflagellata, then the sexual reproduction, the segmentation of the ovum, and the formation of the two germ-layers, must be processes analogous, and not homologous, with the similar processes in Metazoa. For my part I must confess that the second assumption seems to me at present the hardest to swallow. The theory of the metazoan nature of sponges offers in the present state of our knowledge fewer difficulties than the theory of independent descent from the Choanoflagellata. Whether or not a closer acquaintance with the structure and development of sponges will confirm this view remains to be seen. How cautious we should be in pinning our faith to either one of these positive views is sufficiently shown by the history and present position of the cœlenterate theory.

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# THE DISEASES OF THE SUGAR-CANE.

## PART II.

THE first part of the present essay<sup>1</sup> was devoted to a consideration of the general character and prevalence of diseases in the sugar-cane. An attempt was made to determine whether this tropical plant, cultivated for thousands of years, is in reality more subject to the attacks of parasites in the present day than in past times. And the conclusion arrived at was that, although the diseases were in many cases severe and widespread, there was no good ground for supposing that the cultivation as a whole was threatened from this cause.

It is none the less evident that, in the economic crisis through which all sugar-growing countries are at the present moment passing, disease phenomena cannot be neglected. It may well be that estates, just able to hold their own against the severe European competition, would have the scale turned against them by any unhealthiness in their canes. The study of the pathology of the cane-fields must therefore go hand in hand with the improvement of machinery and reduction of expenses now acknowledged to be absolutely necessary.

In the present article it is proposed to discuss the way in which this problem has been attacked in the Tropics. Amid the general apathy of the planters, good hard work has been done by the few who foresaw the threatening danger; and the scientific men in our own, as well as in other countries, have spared neither time nor labour in their endeavour to improve the general agricultural condition of the cane plants. Attention was, in the first instance, devoted almost entirely to animal parasites; and the remedies suggested were drastic, and pointed directly at their extermination. It was proved later that fungi of various kinds were attacking the canes as well; and for a

<sup>1</sup> Barber (1).

time attention was exclusively paid to these vegetable parasites. Lotions and sprays, destructive manures, digging up and burning were the order of the day. It is now being gradually recognised that success by these *direct attacks* is beyond the powers of man. *Indirect methods*, having in view the strengthening of the cane's constitution, are in vogue, on the principle of "less poison and more circumvention". The adaptation of the different varieties of the sugar-cane to soil and climate are more carefully weighed : fresh varieties are introduced and attempts are being made to obtain new and improved strains by means of vegetative and sexual selection.

2. The literature dealing with the *direct remedies* is immense and it will serve no useful purpose to attempt to summarise it, especially as many of the earlier suggestions were made without a knowledge of the true cause of the disease.

In the days when plagues were attributed to the malign influence of supernatural powers, the cure consisted in religious assemblies and votive offerings. We thus find it recorded by Oviedo and Herréra that the whole island of Hispaniola was subject in the early days of cane cultivation to the attacks of a species of ant, which in 1518 overran the island, devouring all vegetation, causing famine to the inhabitants, and nearly depopulating the island. "In order to get rid of these scourges, great processions and vows were made in honour of St. Saturnin ; the day of the saint was celebrated with great solemnities, and *the ants disappeared afterwards gradually.*"<sup>1</sup>

The "sugar-ants," *Formica omnivora*, which appeared in immense quantities in the cane-fields of Barbados and other islands in 1760 were, on the contrary, attacked by the planters with the greatest ferocity—the latter not appearing to have any superstitions in the matter. Poison and fire were freely employed. Corrosive sublimate was found to be most effective, the ants becoming insane and pulling one another to pieces. Burning charcoal was quickly extinguished by the immense numbers which threw themselves

<sup>1</sup> Schomburgk.



upon it. Pits were accordingly dug at intervals in the cane-fields, and a fire made in each. The flames were quickly smothered, the place of each being marked by a heap of dead ants the size of a mole-hill. These direct attacks appear to have been entirely unsuccessful, and the ants only disappeared after a hurricane in 1780.<sup>1</sup>

A distinct advance is to be noted in the advice given by S. Martin Senr., about the same time, with regard to the "blast," probably an aphis, attacking the canes in Antigua. He recommended the use of "wooling raggs dipped in soap-suds after having been used in washing cloaths"—an early reference to the spraying of plants so widely adopted at the present day.<sup>2</sup>

3. The remedies applied during more recent years have usually borne directly upon the natural habits of the pest. A careful study has now been made of the life-history of many of the parasites, in order to select the stage in which the application of insecticides and germicides would be most successful. This varies considerably in different cases. The grub appears to be the point of attack in the moth-borer, the freshly hatched young in the scale-insect, the egg-cases in locusts, and the adult beetle in the Java pest, *Apogonia destructor*. Although the life-history of the latter has not apparently been determined beyond dispute, it has been very carefully studied by Kobus,<sup>3</sup> Zehntner,<sup>4</sup> and other zoologists, and may serve us as an example.

There are usually two main flights of mature beetles, one in November and one in March. The larvæ attack the cane roots between these dates, the injury first becoming noticeable in January. The larger, November, flight is determined by and closely follows the west monsoon, which also brings the first rains. Beetles collected during the last days of October have very immature generative organs and no food in their alimentary canals. They feed at night upon various leguminous plants (*Sesbania*, *Arachis*, *Soja*, *Tamarindus*) and push themselves under the loose earth at sunrise. Specimens dissected in the early days of November frequently have well-filled digestive organs, and, later in

<sup>1</sup> Schomburgk.      <sup>2</sup> Martin      <sup>3</sup> Kobus (1).      <sup>4</sup> Zehntner.

the month, the generative organs mature, and copulating specimens may be captured. The eggs are laid in moist earth and hatch in six to eight days. The larvæ feed on the cane roots for a couple of months or more, as many as sixty having been found upon one plant. The pupal stage lasts for a week, and the beetles, emerging, cause the March flight. These, on dissection, are seen to have empty alimentary canals, and extremely rudimentary generative organs. After feeding for a certain time, the beetles now cease to leave the ground at night, are less abundant as the east monsoon (April) brings the drier weather, and later disappear till the succeeding west monsoon, with its rains, causes a sudden resurrection. These observations point to a yearly brood of young in December. The means adopted is, therefore, to catch the beetles when they appear after the rains, and before they have laid their eggs.<sup>1</sup> Enormous numbers are obtained by shaking the leguminous plants near cane-fields over sheets at night, and large quantities are also obtained by loosening the earth under such plants during the day.<sup>2</sup>

The collection of moth-borer grubs is carried on in the young cane-fields. Plants attacked are readily noted at that stage and destroyed with their contained grubs. Later on, when the canes become large, it is difficult to penetrate the fields, and, furthermore, it is difficult to obtain a cane which is not attacked, so that the destruction of infected canes when well grown would practically mean the reaping of the whole crop.<sup>3</sup>

This destruction of moth-borer grubs and mature Wāwālan beetles before they lay their eggs may be taken as typical of this class of carefully thought out remedies. The indiscriminate liming, trashing, treatment with insecticides and burning have less to be said for them. Owing to the nature of the growth of the sugar-cane, its parasites are peculiarly inaccessible to ordinary methods of treatment. The burning of fields is frequently the only means of reaching them, and this is a step with very grave consequences in the Tropics, because of the destruction

<sup>1</sup> Zehntner.

<sup>2</sup> Barber (1), p. 301.

<sup>3</sup> Watts.



thereby of the carefully fostered moisture-yielding humus. Consequently this method is not recommended or adopted excepting in extreme cases.<sup>1</sup>

4. A more promising field of activity seems to be opened up in the encouragement of the enemies of parasites. We know, for instance, that the moth-borer itself has many minute enemies which feed upon it and tend to keep it in check.<sup>2</sup> Is it possible so to increase these latter as to render the very existence of the moth-borer doubtful?

But success in this direction is accompanied by many difficulties, and needs comprehensive knowledge of the interdependence of the various forms of animal and vegetable life.

One of the most interesting examples of this class of remedies is the recent introduction of the *Mongoose* from India to the West Indies, for the purpose of ridding the fields of the swarms of rats which destroyed great quantities of ripe canes. The experiment, suggested so long ago as 1814 by Lunan,<sup>3</sup> may be regarded as having been successful in the main; although its most ardent supporters cannot claim that the success has been unqualified. The rats have, it is true, disappeared from the fields; but the mongoose, having enormously increased in numbers, has turned its attention elsewhere for food. Not only are the poultry-yards boldly attacked, but game and all sorts of ground birds and lizards have almost disappeared. Urgent appeals have now been addressed to the Governments of various islands to take measures to destroy the mongoose. Its introduction has disturbed the balance of nature. The native insect-destroyers have been decimated, and many see in this one rash step the cause of all the ills of the cane-fields! The introduction of a few pairs of mongoose has produced results neither dreamt of nor desired, but probably legislative action will be futile. The animals have apparently reached their limits as regards numbers, and the judicious introduction of tree-nesting insectivorous birds might do much towards recovering an equilibrium.<sup>4</sup>

An interesting attempt is recorded to inoculate the rats

<sup>1</sup> Harrison (1).    <sup>2</sup> Barber (1), p. 308.    <sup>3</sup> Lunan.    <sup>4</sup> Mongoose.

of Mauritius with a mouse disease—without apparent success.<sup>1</sup>

Nothing appears to be done in the way of encouraging the various enemies of the moth-borer. The small egg-destroying *Hymenoptera* may be left to their good work, but no means suggests itself of increasing their powers. An attempt has been made by Watts to inoculate the moth-borer caterpillars in Antigua with the spores of *Isaria Barberi* and also of *Botrytis tenella* received from Giard in Paris.<sup>2</sup> Similar attempts have been made with Java moth-borers, and by Kobus with the beetle *Wāwālan*.<sup>3</sup> These have not thus far proved successful. It seems, after all, as if little, if anything, can be accomplished along this line of attack. The mutual relations of the various members living in any one district must be much more clearly traced: the laws by which certain forms suddenly increase out of all proportion and without apparent reason during a single season: the conditions which lead to their almost total destruction by parasites—all these must be better understood before we can hope to sow diseases and call epidemics into being, and by this means protect our cultivated plants from their parasites.

5. A useful defensive measure is sometimes found in the careful demarcation of disease areas and the observance of strict quarantine. The introduction of plants from one region to another is rendered dangerous by the remarkable fact that the diseases which attack cultivated plants in one country are frequently harmless in others and *vice versa*,—that the virulence of a disease in any one plant varies with the locality as well as at different times in the same locality. Great care is therefore necessary lest the importation of new varieties into any district should lead to the introduction of new diseases. A striking warning is met with in the history of the replacement of European vines by American ones. The leaves of the latter were found to be more resistant to the vine mildew (*Oidium Tuckeri*), and were consequently introduced into Europe.<sup>4</sup> The appearance of these American vines in Europe was followed, in

<sup>1</sup> Boname. <sup>2</sup> Giard; Wakker. <sup>3</sup> Kobus (2), (3); Wakker. <sup>4</sup> Esser.



1863, by *Phylloxera vastatrix*, a coccid which was known to be present on the roots of American vines. In Europe, however, its attacks on the roots of the vine were much more virulent. It is estimated to have cost France alone many times as much as the war indemnity paid to Germany. In 1877, the continued importation of American vines brought over *Peronospora viticola*, a parasite even more deadly than the *Phylloxera*. In each of these cases a parasite was thrust into the midst of a cultivation utterly unprepared by natural selection to withstand its attacks—a result which would certainly have been avoided with careful legislation on the free distribution of cultivated vines.

The Mallow disease, *Puccinia Malvacearum*, introduced into Europe from Chili, affords another example of the amazing damage which a mild parasite may cause if introduced into a new country.<sup>1</sup> For some years there did not probably exist an exposed Malvaceous plant in Europe which was not severely attacked. In certain localities, it will be remembered, hollyhocks could not be grown because they were destroyed by *Puccinia* before reaching the flowering stage.

It is quite certain that many cane diseases have been propagated in this way. As will be seen later, it is an established custom in many parts of the world to send cane plants from one district to another, since by this means a better growth is obtained. Cane plants thus introduced from Ceylon into Mauritius are supposed to have caused the severe epidemic of borer grubs already noted.<sup>2</sup> These facts, and others of a similar nature, have led to a carefully marked out system of plant distribution in Java. It was found that plants brought from the mountains and planted in the plains were much less liable to sereh. It was further noted that certain districts were comparatively free from sereh. These parts of the island were marked off and placed under strict protection. No cane plants whatsoever were allowed to be introduced into the free regions, whereas plants were freely supplied from them to the plains. Thus we read successively of three more or less sereh-free regions,

<sup>1</sup> Cooke.

<sup>2</sup> Bojer.

Malang, Tangerang and Preanger.<sup>1</sup> Severe penalties have been enforced against planters disregarding the quarantine regulations, and a constant supply of sereh-free plants has thus been obtained to stock the fields and nurseries of infected districts.

6. It is worth while noting, however, that direct attacks upon a parasite are usually futile. It is difficult to point to a single instance in which a widely distributed pest has been stamped out by these means, and it is not usual to pay much attention to a disease until it is widespread. And this has led the students of plant pathology to turn their attention in another direction. Is it not possible so to strengthen the plant as to render the parasitic attacks harmless?

This may be attempted in two ways ; by the perfect adaptation of a plant to its surrounding conditions of growth, and by the encouragement in a plant of some peculiarity which is distasteful to the parasite. In the former case careful attention must be devoted to external surroundings so as to produce healthy, vigorous growth ; in the latter it is necessary to produce a new variety. In nature both of these principles are unceasingly at work ; among cultivated plants it is needful to see that they are not absent.

7. The choice of climate, class of soil, mode and efficiency of cultivation and manuring require constantly to be considered.

The cultivation of any plant in a climate unsuited to it produces a weak form liable to disease. The value of the larch as a timber tree has led to its being planted far beyond its natural limits, with the resulting appearance of a dangerous disease—the larch canker. It would be idle to ignore the fact that different varieties of the sugar-cane vary much as to requirements of soil and moisture. While some, such as the *Bourbon*, are best grown in clayey soils with a considerable amount of rain, others, such as the *Transparent* kinds prefer a light volcanic well-drained soil.

The result of growing the much-valued *Bourbon* in

<sup>1</sup> Kobus (4), (5). Werot (1).



unsuitable places was well exemplified in the recent outbreak of shot-borer (*Xyleborus perforans*) and rind-fungus (*Trichosphaeria Sacchari*) in St. Kitt's cane-fields. The island was roughly divided by an imaginary line across the mountains into the region under *Bourbon* and that under *Caledonian Queen* (a transparent cane). The former cane found many admirers, although clay is unknown in the island (except a few acres above the limits of cane cultivation), and the soil consists everywhere of deep layers of volcanic ash. A careful examination of all the estates in the island showed the diseased area was roughly that of the *Bourbon* cane, the estates under *Caledonian Queen* being practically free from injury.<sup>1</sup>

8. The general character of the cultivation is of equally obvious importance. There is no question that the cultivation in most sugar-growing countries has vastly improved in the last quarter of a century; and very possibly this is the reason why many diseases, formerly abundant, are now of little account.<sup>2</sup> The epidemic of *rust* in Queensland has been referred to careless cultivation, following upon too great success in the first opening up of virgin soil.<sup>3</sup> Two root parasites, *Alectra brasiliensis*<sup>4</sup> in Dominica and *Striga euphrasioides*<sup>5</sup> in the Central Provinces of India, both belonging to the *Scrophulariaceæ*, are found to thrive in waste, neglected cane-pieces, but disappear when the land is kept in order. The *gumming* of Pernambuco has been traced by some as primarily due to bad drainage and condition of soil.<sup>6</sup> The most fruitful cause of cane-disease in India is stated to be the carelessness following years of great prosperity.<sup>7</sup>

On the other hand, good cultivation is not always a remedy for disease. Certain epidemics among the canes are due to other causes than the mere supply of proper nutriment to the plant. The utmost care in cultivation has had small effect for instance upon the *gumming* in Mauritius, the *serek* in Java or the *rind-fungus* in the West Indies.

<sup>1</sup> Barber (2).      <sup>2</sup> Barber (1) p. 311.      <sup>3</sup> Barber (3).      <sup>4</sup> Barber (4).

<sup>5</sup> Watt.

<sup>6</sup> *Sugar-Cane*, 1894, xxvi., 377.

<sup>7</sup> Watt.

9. The question of manuring is a difficult one. Many have put down the increase of disease in the cane-fields to this cause. A lack of adjustment between stimulating and feeding manures will certainly lead to crops of small resisting powers; and little trouble has been taken in the past to determine the needs of the plant in different soils. Scientific manuring will vary with almost every field, depending not only on the chemical composition of the soil, but also on its physical condition. In the great majority of cases, general cane manures have been used without special study of the soil, resulting in waste and, possibly, injury to the plants. But while artificial manuring has probably been harmful in certain cases, the principle is sound enough; and those have far more reason on their side who trace the prevalence of disease to the exhausted condition of the soil on the worn-out estates where manuring has been neglected. The careful comparison of the effect of different combinations of manures upon certain selected canes has been a subject of special study in the various *sugar experimental stations*.<sup>1</sup> A mass of facts has thus been accumulated which should place every planter in a position to test the requirements of his own fields. No praise is too high for the patient manner in which the various Government analysts have pursued these studies, frequently amid the ill-concealed hostility of the planting body.

It is well known that excessive nitrogenous manuring renders *corn* more liable to *rust*;<sup>2</sup> and a similar observation has been made regarding the sugar-cane. In some carefully conducted experiments on a Demerara sugar-estate to determine whether any relation existed between disease and manure, Harrison has demonstrated that the amount of disease was largely proportional to the nitrogen in the manure.<sup>3</sup>

10. A good deal of study has been devoted to determining the chemical constitution of the cane at different periods of its growth,<sup>4</sup> as well as the comparative composition of healthy and diseased canes, without, however, having at present yielded much result of economic import-

<sup>1</sup> Reports. <sup>2</sup> Berlese. <sup>3</sup> Harrison (2). <sup>4</sup> Went (2); Sagot *et* Raoul.



ance. A careful analysis of diseased canes has been made in various countries, one frequent result being a deficiency of silica in the ash. Stutzer found that the plants suffering from sereh had deficient silica and excess of potash, and suggested that, among other remedies, a rational system of manuring might be applied to sereh.<sup>1</sup> Francis, in canes attacked by rust in Trinidad, found 36·01 per cent. of silica in the ash instead of 45·84 per cent.; and Liversedge, examining Queensland canes also suffering from rust, found the deficiency in silica much greater, the diseased canes containing only 25 per cent. or 30 per cent. of the normal quantity.<sup>2</sup> It does not appear how this state of things is to be altered.

The idea has been advanced in certain directions of altering the cell-sap by the addition of special substances, such as copper sulphate to the soil,<sup>3</sup> and thus rendering a plant more capable of resisting the attacks of a parasitic fungus. But sufficient stress does not seem to have been laid on the selective power of the plant itself. Changes are probably constantly taking place in Nature by which a plant renders its juices less palatable or nutritious to its parasite, but it is doubtful whether any system of manuring will ever succeed in thus directly altering the cell-sap.

11. It is quite certain that the cells of plants are more or less resistant to disease according to their age. Young cells by their greater vitality are able to resist the action of the ferment emitted by an attacking fungus. The older cells, with their stores of reserve materials and less active protoplasm, on the other hand, are frequently guarded by the presence of special substances, *e.g.*, tannin in many cells, ethereal oils, resins, etc. The tendency of cultivation is, however, to eliminate these latter substances; and this will possibly account for the time of appearance of certain diseases.

The rind-fungus, *Trichosphaeria Sacchari*, may be present in the young tissues, but it is one of the characters of the disease that it becomes first evident by the discoloration of the mature joints in the middle of the cane, where

<sup>1</sup> Stutzer.

<sup>2</sup> D'Albuquerque, see also Boname.

<sup>3</sup> Berlese.

the protoplasmic lining of the cells is very thin and the large sap cavity abundantly stored with sugar. The fact that the joints first showing signs of disease are not the lowest and oldest may be explained by the greater exposure of the higher ones (12th or 13th, according to observations of the author), which are consequently more freely tunnelled by the moth-borer, and thus bared for the fungus spores. There is a small step between such cells and those actually dead, and in New South Wales the rind-fungus appears principally to attack canes near the point of death.<sup>1</sup>

The apparent periodicity observed in sereh seems to be due to a different cause. The disease makes its appearance shortly after the rains, because the stricken canes alone refuse to shoot up. The rains again bring about the appearance of the swarms of wawalan in Java, awakening them from their summer sleep. It has frequently been noticed that plant canes and ratoons (second growths from the cut plants, the roots being left in the ground) are differently attacked by disease. The "plants" seem to be more severely affected by gumming and rind-fungus, a fact which may depend on the older and stronger root system of ratoons. On the other hand, in sereh the disease appears to increase steadily all through the life of the plant, being much more severe among ratoons. As a result of this, while ratooning is to be encouraged in places attacked by rind-fungus, it has practically disappeared from Java.

12. One of the most interesting features in the study of cane diseases is the apparent immunity of certain varieties. Taken broadly, the "soft" canes are the ones most liable to disease, while the "hard" canes are more or less resistant. It is not likely that the juiciness of the stem or the hardness of the "rind" is of itself a direct factor in the matter, but it is fair to infer that these characters are among a series of correlated ones which render the plant a more or less easy prey, just as we are told white chickens are more liable to gapes and white verbenas to mildew.<sup>2</sup> The *Cheribon* cane is especially subject to

<sup>1</sup> Cobb.

<sup>2</sup> Darwin.



sereh in Java ; in Mauritius the *Bamboo* cane is most liable to gumming ; while in the West Indies it is the much esteemed *Bourbon* which is principally threatened by the rind-fungus. In each case the predominant cane is most attacked. Each of these three is a “soft” cane. What are the characteristics of such a cane? Large, free-growing, juicy, of great saccharine content, and readily torn by the teeth.

In India the *paunda* or native forms are much the hardiest ; in Java the seedling canes more nearly approaching the *Glagah* or wild indigenous kinds are free from disease. From this it is easily gathered that the less hardy canes are the outcome of the most careful human selection. Canes left more to themselves and the action of natural selection are invariably better able to resist disease. An interesting example of this is met with in the canes grown in India—probably near to, if not itself, the original habitat of the species. The forms cultivated may be roughly divided into two classes—those used in the production of sugar and those eaten as a fruit. The former are small, hard, not very juicy, and are left more or less to themselves at a distance from the houses. The latter are thick, juicy, with a thin rind ; they are planted carefully near the houses, and treated to a garden cultivation. The human selection by which these “soft” varieties have been produced has been one-sided ; it has to a great extent neglected liability to disease. Consequently these canes are severely attacked the moment they are left to themselves, and in the field are utterly unable to compete in hardness with commoner kinds.<sup>1</sup>

This agrees very well with the remark that liability to disease results from an accumulation of certain of a plant's many characters, and that there are all stages between healthy and diseased plants.<sup>2</sup>

13. Attention has already been drawn to the fact that canes are found to be of stronger growth if the plants are occasionally brought from a distance, on the principle that plants, as well as animals, are all the better for an occasional

<sup>1</sup> Watt.

<sup>2</sup> Sorauer.

change of climate and food. This has been a custom from time immemorial among the cane growers of India, and has been extensively adopted in most sugar-growing countries.

It is also a firmly established belief that the long-continued planting of any variety in the same locality is certain to engender a diseased condition. Many interesting and striking examples of this might be quoted. In 1840 the Bourbon cane was introduced to Bogra, one of the chief sugar-growing parts of Bengal. For eighteen years it succeeded remarkably well, and practically displaced the older native varieties, and those who had adopted it became rapidly rich. In 1857-1858 a disease suddenly appeared which left the canes rotting on the fields, and in the succeeding year or two the Bourbon cane disappeared from cultivation.<sup>1</sup>

Cases of this kind—and many others might be quoted—may be explained in the following way. A variety introduced into a new country is at once placed among a new set of parasites. Sometimes these are able immediately to assert themselves, rendering acclimatisation difficult. Others require a certain number of years before they can adapt themselves to the protoplasm and cell-sap of the new variety, after which they rapidly destroy it, unless it has a similar or greater adaptive power. This seems to account for the sudden destruction of the Bourbon cane in the Central Provinces of India. In the same way it was several years before the *Peronospora viticola*, already referred to as coming from America, was able to overcome the natural resistance of European vines. Once able to do so, it became an active and dangerous parasite.

14. We may conclude then that continued planting in the same soil need not cause a deterioration in the cane, especially as there are many districts where the Bourbon has been grown for years without an appreciable increase of disease (as in Demerara). It has been urged by many that the exclusive vegetative reproduction of the sugar-cane, without the chance of an occasional cross, is bringing about a gradual decline of vigour. This may

<sup>1</sup> Watt.



perhaps be the case, but it does not explain the hardness of the resistant varieties which have been propagated in a similar manner. The nearest allies of the sugar-cane among wild forms appear also to be apogamous,<sup>1</sup> so that vegetative reproduction is probably a natural mode of increase. There seems, in fact, to be no more reason for deterioration in the sugar-cane from this cause than there is in oranges, vines, pine-apples, and other fruits propagated in this way.<sup>2</sup>

As far as can be gathered from the past history of these "soft" canes, one of their characters has *always* been that they are especially liable to disease. The first references to the Bourbon cane in Jamaica, India, Antigua, Queensland and Pernambuco seem, indeed, to unite its great value as a sugar producer with a certain tenderness. There seems then to be no valid reason to assume that the canes most prized in cultivation are deteriorating. They are the best results of the careful human selection of centuries. Sufficient care has not been exercised to bring out disease-resisting properties, as well as those of sugar production; but this is a point now held to be of first importance in all sugar-growing countries.

15. The search after new varieties of the sugar-cane is by no means a new one. Selection has been at work for thousands of years, and, thanks to it, we have at present hundreds of varieties, many of them capable of producing excellent results.

Within recent years attempts have been made to determine the limits of asexual or vegetative selection. A series of laborious experiments have been conducted by Edson in Louisiana with the object of finding out whether, by planting the richer canes of a field, a richer variety may be built up.<sup>3</sup>

The results thus far are in favour of such a method in the United States. It has, however, been urged in Java, and elsewhere in the Tropics, that the richer canes of these localities are not capable of improvement to the same extent as the poorer Louisiana canes—the sugar content of the

<sup>1</sup> Sagot *et* Raoul.

<sup>2</sup> Möbius, see also Went (3).

<sup>3</sup> Edson.

*Cheribon* in Java, for instance, being assumed to be near perfection.<sup>1</sup>

Attempts at creating a disease-proof variety of "soft" cane are more to the point. This has engaged much attention in Java, and a certain amount of success has already been attained. The method suggested is the following: Select plants which were living as long as possible before the first general appearance of sereh. The chances are that such plants have a more or less resistant character. Form a new plantation from the best of these, using only perfectly sound canes for planting. Constantly weed out those attacked by sereh.<sup>2</sup>

16. The principal objection to this method is its slowness. A more rapid, but less reliable, means of obtaining a new variety is by *bud-variation*. It occasionally happens that a plant produces a bud quite different from the rest in foliage and other characters. If the shoot thus produced can be used for propagation, a new variety will probably be obtained, because its peculiarities will remain fixed as long as the vegetative method is adhered to. If, however, the variety thus obtained is allowed to seed, it at once loses its assumed characters, and tends to revert to the parent type. It is exceedingly rare that such a variation is detected in the sugar-cane, and the probability of its occurring in an entirely useless direction practically removes bud-variation from available methods.

Another possible way of obtaining new varieties asexually is by what are known as *graft-hybrids*. This subject appears, however, to be rather obscure, and the cases in which success is claimed do not always bear very close examination. It occasionally happens that in grafting a shoot arises from the point of union of stock and scion, presumably by fusion of the parent cambiums, and unites the characters of the parents. It will be seen at once that graft-hybrids must be of rare occurrence, when we consider that the operation of grafting is principally performed when it is desired to perpetuate the characters of the scion unaltered. There seem to be authentic cases of varieties arising in this

<sup>1</sup> See *Sugar-Cane*, 1894, xxvi., 73 and 271.

<sup>2</sup> Went (4).



way. Attention is drawn to it in this place because of recurring statements as to the value of this method in certain sugar-growing countries. In the absence of the means of determining their truth, it is useful to inquire how far grafting will succeed in Monocotyledons, where there is no cambium, and especially whether the sugar-cane is amenable to this treatment.<sup>1</sup>

17. The main lines along which selection must be followed are, however, by the production of seedlings. It is a noteworthy fact that many varieties of plants, especially cultivated ones, cannot reproduce true from seed. Of ordinary fruit trees, for example, small, sour, and uneatable fruit are borne by 90 per cent. of seedling peaches, 93 per cent. of plums and 97 per cent. of pears and apples.<sup>2</sup> New varieties are therefore certainly and readily obtained by crossing; it is also patent that such varieties are in the great majority of cases useless reversions to an uncultivated or natural condition of the plant.

The variability of the sugar-cane has been amply demonstrated among the collections of spontaneous seedlings as well as those raised by artificial crossing.

For many years the cane was held to be incapable of producing fertile seed. This is the more remarkable because many eminent botanists have paid special attention to the subject both in India and the East and West Indies. In all probability multitudes of seedlings have been produced year by year in favourable localities; but from some cause, perhaps their similarity to grasses, no one succeeded in detecting them.

The arrowing or flowering of the cane is a very well-known feature in tropical scenery, yet in parts of India, where the sugar-cane is grown, the flowering is of very rare occurrence. It is mentioned by Dr. Kobus in his account of his journey to Saharanpur to obtain new varieties for cultivation in Java, that he met with people who had never seen the arrows, and did not know in what part of the plant

<sup>1</sup> Barber (5); see also Darwin, Sorauer, and *Louisiana Planter*, April 17, 1897.

<sup>2</sup> Went and Geerligs.

to look for them. Whether this was at all a common occurrence or not, it is certain that the arrowing of the cane was regarded with superstitious dread. Brahmins have been known to desert a district in which it occurred.<sup>1</sup>

This constant cutting of the canes before the flowering period arrived, and the consequent absence of arrows, has undoubtedly tended to strengthen the belief in the non-fertility of cane-seed. It is now regarded as probable that the sugar-cane has never entirely lost its seeding powers; and there are some who believe that the immense number of varieties which have gradually crept into existence are not bud-varieties but true hybrids.

18. Experiments with seedling canes have now been carried out in every quarter of the globe. Excellent varieties have been reared by crossing; and the nature of seedling canes and the means of obtaining them is well understood. Yet it is barely ten years since the fertility of cane seed became a recognised fact.

The discovery of cane seedlings appears to have been made in the island of Barbados,<sup>2</sup> where we learn that a planter named Parris, in 1858, observed great numbers of seedlings which he carefully reared, but rejected because of the appearance of certain objectionable characters. In spite of the authentic records of this fact, as well as less certain statements regarding the discovery of cane seedlings in Java a couple of years later, the fertility of cane seed was again disputed and these observations almost forgotten.

Natural seminal reproduction seems to be particularly favoured by the climatic conditions in Barbados, whereas in Java the reverse appears to be the case. Soltwedel in the latter island made crossing experiments for years, besides carefully searching the fields, before he succeeded in 1886-87 in proving to his own satisfaction that he could thus produce hybrid canes. In Barbados, on the other hand, a search in the fields by Harrison and Bovell was rewarded by the discovery of many thousands of plants in January, 1888. While the Java results were not made public for several

<sup>1</sup> Watt.

<sup>2</sup> Kobus (6). See also especially *Kew Bulletin*, Oct., 1891.



years, those of Barbados were quickly known all over the world in sugar-growing countries and excited the keenest interest in the subject. In Barbados, Harrison and Bovell, and later, in Demerara, Jenman and Harrison have continued the study of cane seedlings, and to their valuable reports we owe most of our present knowledge on the subject.<sup>1</sup>

The results are, on the whole, satisfactory. As the sugar-cane requires two years for its growth from seed to flowering, seminal selection here is slow work; and those who failed to grasp the subject, and looked for a sudden revolution in the cane-fields, were from the first doomed to disappointment. From the nature of the case, experiments must be conducted on a large scale—a difficult matter with so extremely tender a seedling which grows into so large a plant. Any one reading the Demerara reports will be at once convinced of the proportions of the task set themselves by Harrison and Jenman; and the comparative failure of all but a few attempts elsewhere adds to our sense of the difficulty of the work.<sup>2</sup>

Two main features have constantly to be held in view in these experiments. The variety aimed at must have a sugar yield equal to the best of the old sorts, and it must have a greater power of resisting disease.

The following plant, raised by Prinsen Geerligs in Java, may serve as an example of a hybrid sugar-cane. Of the parents, the *Black Java* cane has infertile pollen and therefore no seedlings of its own; it is much planted because of its rich juice, but it cannot withstand sereh. The *Canne morte* of Australia is vigorous and resists sereh, has a great quantity of sugar and yields heavy crops, but its juice is of inferior sucrose content. The hybrid obtained shows very vigorous growth, with good yield of juice of good quality.<sup>3</sup>

Careful experiments, conducted in this way, are sure ultimately to succeed in producing valuable additions to the varieties of sugar-cane in cultivation, and also to assist in checking the dangerous parasitic diseases to which the better-class canes are liable.

<sup>1</sup> Reports.<sup>2</sup> Reports.<sup>3</sup> Geerligs.

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## RECAPITULATION.

ONE of the commonest errors, or fallacies in science, at any rate in biological science, is hasty generalisation. A statement which is observed to be true in particular cases is frequently stated to be generally true, and the generalisation is widely accepted and commonly taught until some independent critic arises to point out that there are important cases in which it does not hold. The Haeckelian generalisation that individual development is a recapitulation of ancestral development is an example of this. It has been current in various formulæ. Haeckel called it the biogenetic law. Professor Milnes Marshall, I believe, was responsible for its expression in the form that each individual is compelled to climb its own genealogical tree. The pre-Haeckelian statement due to Von Baer was that animals resemble one another more in the earlier stages of their development, and diverge in form as they approach the perfect or adult condition. Mr. Adam Sedgwick has lately attracted considerable attention by a trenchant criticism of the generalisation in all these forms, and has put forward conclusions which are incompatible with it, and which I propose to consider in the course of this article. But it is certain that the doctrine in question has never been supposed by modern working biologists to be literally and universally true. If it were so we should be able to discover the complete evolutionary history of any animal from an examination of its individual development, which is notoriously not the case. In fact it is admitted at the present time by every investigator of evolution that whatever hopes may have been formerly entertained concerning the revelations to be obtained from embryology, we have not obtained, and cannot obtain, from a knowledge of ontogeny or the development of the individual, anything more than occasional indications of phylogenetic history, or the modification of the series of generations. Our great English embryologist, years ago, in his classical text-book,

expressed the truth of the matter when he stated that ancestral stages were liable to be dropped out or omitted in embryonic development, to be hidden or replaced by new characters in larval development. We have long been accustomed to use technical terms to distinguish ontogenetic characters which are probably or evidently recapitulative, from those which have evidently been recently evolved in the larva or embryo: we call the former palingnetic, the latter kainogenetic. What is new therefore in Mr. Sedgwick's paper is not the proposition that ancestral structure is not always recapitulated in the early stages of individual history, or that many embryonic or transitory characters are not ancestral. The main object of the paper is to support a particular explanation of the apparent capriciousness which is observed in the persistence or disappearance of ancestral organs and characters. This explanation is that the retention of an ancestral condition in the series of embryonic changes indicates that this condition was once a larval condition, that is to say, was retained as a necessary adaptive character in a free-living larval stage of the animal, after the new adult character had been evolved. Afterwards the larval stage ceased to be free, the young animal being confined either in an egg-shell or in the maternal uterus until its metamorphosis had been accomplished, when it was hatched or born with a structure more or less exactly similar to that of the adult. On the other hand, according to Mr. Sedgwick, when a change occurs in evolution in an animal which has no larval stage, in other words when a new adaptation is produced which is related to conditions existing throughout the independent life of the organism, then this variation or modification affects the whole constitution of the individual, has a retrospective influence on the embryonic development, and comes to be developed directly with no, or scarcely any, trace at any embryonic stage of the structural condition which must have preceded it in the line of descent. The two most marked instances of these contrasted modes of development cited by Mr. Sedgwick are (1) the existence of gill-clefts and gill-arches in the embryos of all air-breathing



vertebrates, and (2) the absence of any trace, in embryonic life, of the fore-limbs in snakes.

Embryologists will be aware that the theory so ably advocated by Mr. Sedgwick had already been suggested by Balfour. It is contained in the following paragraph (*Comp. Embryology*, vol. ii., p. 174):—

“Another point which deserves notice in the snake is the absence in the embryo of all external trace of limbs. It might have been anticipated on the analogy of the branchial arches, that rudiments of the limbs would be preserved in the embryo even when limbs were absent in the adult. Such however is not the case. It is however very possible that rudiments of the branchial arches and clefts have been preserved because these structures were functional in the larva (Amphibia) after they ceased to have any importance in the adult; and that the limbs have disappeared even in the embryo, because in the course of their gradual atrophy there was no advantage to the organism in their being specially preserved at any period of life.”

Mr. Sedgwick has not extended his criticism to the question of recapitulation in larval stages themselves.

This however has been done by Mr. E. W. Macbride, who points out that according to the view we have been considering, however modified the record of ancestral history contained in the larval development may be, the embryonic record can never rise above it in value. This writer evidently, whether consciously or unconsciously, takes a Lamarckian view of evolution. He considers that so far as we can judge by comparative anatomy the stimuli to evolution, in the sense of change of structure, have been two (1) change of environment or habits, (2) increased or decreased demands on the working of certain organs. Larval stages according to Macbride are due to new stimuli commencing to act at a late period of life; in the case of flat fishes if the young when they emerge from the egg were at once to adopt the adult mode of life then their symmetrical larval stage would be omitted from their ontogeny. He considers that secondary larvæ must be regarded as having arisen owing to the young adults having taken to a new mode of

life. He instances as the best examples of this the aquatic larvæ of May-flies and dragon-flies, which have gills consisting of thin laminæ abundantly supplied with tracheæ. He then proceeds to consider in some detail the numerous larval forms of Crustacea and Echinodermata, and to draw conclusions concerning their ancestral significance.

We have then to rely for our conclusions concerning the evolutionary history of a form, or the course of modification it has passed through in descent, on the evidence of comparative zoology and palæontology, and in tracing lines of evolution and comparing them with the changes exhibited in the development of the individual, we are necessarily led to inferences concerning the modes in which modifications are produced. Conditions and structures exhibited in the embryo which are absent in the fully developed organism are in some cases, as we have seen, repetitions of a larval or temporary condition of the immediate ancestor. Further we know that in numerous cases such a larval stage is secondary and not itself an ancestral condition. Therefore neither the embryonic transient stage nor the larval stage by any means necessarily exhibits a condition of any adult ancestor. The general truth which we do find to hold good is that well-marked larval stages are associated with conditions of life differing from those to which the adult is subjected. Metamorphosis in the structure of the organism is observed to correspond to a more or less sudden and considerable change in the conditions of life. An organism may be adapted to one set of conditions throughout its independent life, or successively to different sets.

The fact that all the terrestrial Vertebrata, the Sauropsida and Mammalia, exhibit gill slits in the embryo at a certain stage is explained by the fact that they are all descended from ancestors which passed through an aquatic larval stage. The Amphibia at the present day pass through such a stage. It does not follow that the Amniota are descended from ancestors which were aquatic and branchiate in their adult condition. The actual history of the Alpine Salamander (*Salamandra atra*), shows us how, as an adaptation to terrestrial conditions, the offspring may be



retained in the uterus during the branchiate condition, and not be born until the metamorphosis has been accomplished. We have good reason to believe, however, that the transition to the Amniota from Amphibian-like ancestors was not effected in this manner, since viviparity even in Mammals was evidently acquired at a later stage, and the change came about by means of the development of an egg-shell in which the larva was contained and protected during its development. None of the existing Amphibia, though they exhibit various different methods by which the eggs are kept out of water during development, show any tendency to form an egg-shell. But it may reasonably be suggested that the formation of this structure was originally due in some way to the stimulation of the epithelium of the oviduct by the retention in it of a large-yolked ovum. Mr. Macbride distinguishes two classes of stimuli to evolution, change of environment, and increase or decrease of function, but it appears to me that all modifications may be described as the effects of stimulation, of which the increased or decreased activities of organs are particular cases. To my mind it is not possible to conceive the origin of the shelled egg as due to the selection of individuals in which the shell appeared as a variation, unless we have some idea of the cause of its appearance.

Judging from the structure of the aquatic larvæ of existing Amphibia, and from the general requirements of aquatic life, we may suppose that in the actual ancestors of the Amniota the free aquatic larvæ possessed a median membranous fin-fold. We do not, however, find that this or any trace of it is preserved in the embryo of the Amniota. Lateral fin-folds do not exist in the tadpole of the Batrachia, and we need not expect, therefore, to find them in the embryos of Amniota. But the disappearance of the median fin-fold indicates that the ancestral larval condition may undergo considerable modification when it becomes embryonic. The mere fact that they were functional originally in a free larval condition is probably not the whole explanation of the temporary development of a complete system of gill-arches and gill-slits

in the amniote embryo. Supposing that no functional importance in embryonic life belongs to them, it is to be noted that the embryonic branchial blood-vessels are metamorphosed into the vascular system of the adult, as they are in the metamorphosis of Amphibia, and a very considerable and very important part of them persists in the adult structure. This does not account for the persistence in the embryo of open branchial clefts, but even these do not wholly disappear in development. The first remains as the Eustachian tube, and even the posterior are related to the development of the thymus gland. It seems to be a general fact that a structure which in metamorphosis disappears completely may easily be omitted altogether in embryonic development, while one which is modified into something else continues to pass more or less through its original larval condition.

If the aquatic larval condition then was ever an adult ancestral condition it must have been the ancestor of Amphibian forms, and only through these the ancestor of the Amniota. We have therefore to inquire how far the larvæ of the Amphibia resemble the adult ancestors of that group. The important resemblances of a tadpole to a fish, and the evidence that fishes are older palæontologically than Amphibia, are sufficient to show that the latter are descended from fishes, and that the aquatic larva is not entirely a kainogenetic adaptation. But when we come to compare in detail the Amphibian larvæ with all known fishes we are forced to the conclusion that the larva is far from repeating any possible adult condition very exactly. If we suppose that the tadpole of the frog represents the adult ancestor of that form, we imply that that ancestor was entirely destitute of fin-rays and of paired limbs, and that the fore-limbs were originally evolved as outgrowths within the branchial chamber beneath the operculum. We should also imply that the piscine adult ancestor had no scales. Now the recent Dipnoi present an obvious approximation to the Amphibia, and we know that forms belonging, according to the structures capable of preservation in the fossil state, to the Dipnoi existed as early as the Devonian period. We do



not know how the paired limbs were transformed from the radiate to the pentadactyle form. But we consider it most probable that the Amphibia diverged at an early period from the Dipnoan stem, and therefore arose from ancestors which had fin rays in a continuous median fin, which possessed paired limbs like those of the Dipnoans, and scales or dermal ossifications. It is more probable that the Amphibian larva has lost its paired limbs and fin rays since the adult form was evolved, than that the adult ancestor never possessed paired limbs and that the pentadactyle limbs were evolved independently of the paired fins of the Dipnoi. The Amphibian larva has also lost all trace of scales or other dermal ossifications. The extinct Amphibia called Labyrinthodonts possessed dermal osseous plates, and the existing Cœciliidæ possess scales. The larva of the frog therefore, instead of recapitulating the ancestral condition has lost nearly everything characteristic of a fish except the pharyngeal branchiæ, which it could not lose without ceasing altogether to be an aquatic larva. The larva therefore is much more of an adaptation than a recapitulation.

At a time when the doctrine of recapitulation had more influence on phylogenetic inquiries than it has now, W. K. Parker observed characters in the tadpole of the Anuran *Xenopus* (*Dactylethra*) which he considered more obviously ancestral than those of the common frog. He regarded the skull and the tail as remarkably chimæroid. The tail he said terminated in a long pointed lash, the fin membrane ceasing at some distance from its end. Mr. Beddard found on examining specimens of this tadpole hatched in the Zoological Gardens, that the fin membrane really continued to the extremity of the tail, but was very narrow, and the description of Parker was a mistake due to the contraction of the membrane in spirit specimens. There are other peculiarities however in the *Xenopus* tadpole in which it differs from the larva of the frog. The mouth is terminal, there are no suckers on the chin, and the fore-limbs do not develop beneath the opercular fold. These differences show so many features in the frog larva which must be regarded as special modifications in that form.

We must infer from these facts that the Amphibian larva only resembles the ancestor so far as the conditions of its life resemble those of the ancestor, and differs so far as its conditions of life are different from those of the ancestor. Selectionists of course will see nothing in this inconsistent with their views of modification. They will say that the larva and the adult have varied independently and the fittest have survived in each case. But in this as in many other cases it is important to notice that we have no evidence that the required variations ever occurred except when the conditions of life changed. The mere statement that the modifications occurred and survived because they were advantageous is not sufficient. Supposing that the modifications occurred in certain individuals while all the rest died, then we ask how and why did they occur in those individuals. So long as we regard the individual as a single definite form like a house or a vase, it may appear conceivable that the modifications of individuals are due to changes arising in the germ cell, to blastogenic variations, and that the adaptation of individual to conditions of life is due to the selection among a host of slightly different individuals of those which most approach the suitable structure. But when, as in the case of the frog, we see the same individual always passing in development through two quite distinct stages of life, which are adapted to two incompatible conditions, aquatic and terrestrial, we find it much more difficult to form a conception of the mode in which such a metamorphosis could have been brought about by blastogenic variations. Supposing it to be possible by always breeding from the individuals with the smallest limbs to produce a race or species without limbs at all, it does not follow that it is possible to produce by selection a race in which there are no limbs during the first half of life, and well-developed limbs in the second half. But this is what we have in the frog. It may be said that the two stages are so marked and distinct as to vary independently as though they were separate races, and therefore a different standard of selection can be applied to each. But this simply means what the Lamarckian contends for, namely, that the modifications are



always associated with differences in the conditions of life. If the conditions of life have nothing to do with the origin of variations then the variations of the fins in the two stages of the Amphibian will be the same as in the Dipnoan which lives under nearly the same conditions all its life. Only the standard of selection will be different. But it is impossible to believe that the selection of individual variations such as occur in the Dipnoans could produce a form in which there were two stages of life, one without limbs and the other with well-developed pentadactyle limbs. There is no evidence that such a thing is possible.

On the other hand we have plenty of evidence that conditions of life acting temporarily during a particular period of life produce definite changes which disappear when different conditions act upon the same individual. Muscles and skeletal structures diminish when disused and increase when exercised. As far as the individual is concerned, apart from inheritance, we know that adaptation of structure to different conditions of life at different periods of life actually does take place. It cannot be denied that the process of evolution so far as we are able to elucidate it is such as would result if such changes as are produced by conditions in the individual were inherited, if successive states corresponding to successive modes of life tended to recur in every generation, so that the effects of conditions were cumulative. The Dipnoan ancestor of the Amphibian was able to respire air by means of its air-bladder. Reaching places where the air was moist, but water in any large bodies scarce in summer, it would be forced to depend more on air breathing, and less on its gills. The latter would be more or less dried and, therefore, undergo retrogressive changes. The air-breathing adult would deposit its eggs in small bodies of water where want of room, the persecution of enemies, and the scarcity of animal food would force the larva to live among water-weeds and live upon them. It would cease to use its paired fins, and cease to exercise the muscles and rays of the median fins. The larva would, therefore, on Lamarckian views, become degenerate. According to those views, development of organs depends

very largely on the stimulation applied to them in the struggle for existence in successive generations of individuals. In the larva of the frog the limbs and fin-rays ceased to be stimulated by exercise, and consequently developed less and less in this period of life. In adult terrestrial life, on the other hand, the paired limbs were constantly used, and the stimulation thus caused would produce its effect at the corresponding period of life in the development of the limbs in the adult form at the end of the larval period.

We may next consider recapitulation in the development of fishes. A classical instance of this is the development of the tail in certain Teleosteans. The primitive condition of the tail is the symmetrical condition, in which the fin membrane is continued round the end of the notochord, and supported internally by cartilaginous rays, outside which, beneath the epidermis, are very numerous thin horny fibrous rays uniformly close together. This condition existed in the earliest Elasmobranchs, for instance in *Pleuracanthus*. In the majority of Selachians from the Carboniferous to the present day, without any fundamental modification of the character of the skeletal ray-supports, there is an alteration of the shape of the fin. The ventral portion is enlarged to a greater or less degree in comparison with the upper, and so forms a ventral lobe of the fin, the original terminal portion forming the dorsal lobe.

In the osseous fishes, which general term includes Ganoids, Teleosteans and Dipnoi, there is an important modification of the skeleton which extends to the skeleton of the tail. Dermal calcifications derived from the scattered tubercles of the Elasmobranchs unite to form bony fin-rays outside the horny fibres. These at the bases of the rays correspond in position to the cartilaginous median rays, while distally they branch and correspond more with the original horny fibres. With the appearance of this modification the tail may retain its original symmetrical or diphyccercal condition as in several Devonian Ganoids, in the modern *Polypterus*, and in both ancient and modern



Dipnoi. In other cases as in the Sturgeon and many other Ganoids the hypertrophy of the ventral lobe produces the heterocercal condition. Finally, in Teleosteans, the upper lobe or original terminal portion of the tail is aborted altogether, and the ventral lobe becomes terminal and acquires a secondary symmetry. It is unnecessary on the present occasion to trace the extent of recapitulation in all the various cases. It will be sufficient to refer to the homocercal Teleosteans, for example, the Pleuronectidæ, Clupeidæ, or Salmonidæ. In these the larva has at first a symmetrical membranous tail without fin-rays. In this minute radiate fibres appear, which clearly correspond to the horny fibres of Elasmobranchs and Ganoids. The cartilaginous rays are but little developed in the fin itself, but the basal portions within the trunk, that is the epural and hypural cartilages are developed and soon replaced by bone. When the dermal fin-rays appear they are from the first developed on the ventral side behind the termination, and the terminal portion never develops them. This terminal portion is bent up by the hypertrophy of the ventral lobe and becomes rudimentary.

Thus in these fishes the tail is at first diphyccercal, then in development passes through a heterocercal condition and afterwards acquires the secondary symmetry called the homocercal condition.

Two zoological thinkers have recently made endeavours to ascertain the advantages of the various forms of fishes' tails in adaptation to different circumstances. They do not refer to the origin of the different forms, but to their mechanical, or adaptational value. This in itself is of great importance and interest, and to the zoologist who thinks in the terms of selection the use or advantage of each form appears to be the explanation of its evolution. F. E. Schultze develops his views in connection with a consideration of the tails of the Ichthyosaurians which are heterocercal, but with an asymmetry which is the reverse of that seen in fishes. The terminal portion of the vertebral column in these reptiles was bent downwards, and on the upper side of it was a somewhat triangular cutaneous fin, in

addition to the dorsal fin in the middle of the back. It is surprising that the true structure of the tail in these animals, discovered by Fraas of Stuttgart in 1892, is not described in that generally excellent work the *Royal Natural History*, where the obsolete view that the tail was horizontal like that of Cetacea is repeated.

Schultze points out that in the heterocercal tail the more expanded lobe is the more flexible, while the continuation of the vertebral column is much more rigid. Consequently when the tail is moved horizontally the flexible lobe will yield to the resistance of the water, and the surface of the whole tail will be inclined to the horizontal plane, and will move not horizontally but towards the more rigid edge, that is in the case of sharks or sturgeon, upwards. Everyone knows that an oar inclined under water and moved horizontally will rise to the surface or go deeper into the water according to the direction of the inclination, and the same thing happens when a feather in which the vane is broader on one side of the axis than the other is moved under water. The greater flexibility of one sides causes the feather or heterocercal tail to take an inclined position and therefore always to move away from the horizontal plane towards the more rigid edge. Consequently the tail of the fish in which the upper lobe is more rigid rises when it moves. As the fish is at the same time propelled forwards, the effect of this would be to ram its snout into the ground, and to counteract this it only needs to raise the edge of its pectoral fins, the resistance of the water will then raise the fore part of the body and the whole fish rises from the bottom. According to Schultze this is the object of the arrangement; the fish being heavier than the water requires a mechanism to enable it to swim easily from the ground. The Ichthyosaur on the other hand was specifically lighter than the water on account of its lungs and blubber, and therefore needed a motor mechanism to counteract its tendency to rise. Its tail when in motion sinks, and it only needed to lower the front edge of its pectorals, to descend to greater depths when it pleased.

The relations of the fins in the flying fishes (*Exocæti*),



and certain other Scombresocidæ are analogous. The tail is homocercal, but the ventral lobe is distinctly larger and stiffer than the dorsal. Physiologically therefore the tail acts like that of Ichthyosaurus. Here however the counter-action cannot be produced by the pectorals, because they are too long and too weak, and moreover are observed to be folded against the sides of the body in rapid swimming. The necessary effect is produced by the pelvic fins, the specific gravity of the flying fish being less than that of the water.

Ahlborn takes a somewhat different view. He considers that there are important advantages in the action of heterocercal tails which Schultze has not perceived. In his opinion the bottom fish requires to have a tail which will rise in order to prevent it rubbing against the ground in its stroke and therefore failing to propel the fish when the latter desires to put itself in motion. In the case of the surface animal, Ichthyosaur or flying-fish, a symmetrical tail might when put into motion at the surface pass into the air, and so the creature would become for the moment helpless; it therefore requires a tail which will tend to pass more deeply into the water. He calls the ordinary heterocercal tail epibatic, the symmetrical tail isobatic, and the tail with reversed heterocercy hypobatic.

It is clear that none of these considerations help us to understand how on Lamarckian principles the various forms of tail arose, and even with regard to function it seems to me that the two authors mentioned have overlooked some of the most important points. It seems to me that the chief use of a heterocercal tail to a fish that lives near the bottom is the very fact that such a tail throws the hinder end of the body up and keeps its nose on the ground, for it is on the ground that it finds its food. It is a remarkable fact that the heterocercal tail is usually associated with a snout projecting beyond the mouth, and such a snout is in a large number of cases, if not in all, used for routing in the ground in the search for food. Such is certainly the case in the sturgeon, and it is true of some at least of the Selachians; *Scyllium canicula* and *catulus* feed on lower

animals which conceal themselves in the ground at the sea-bottom, and probably use their snouts in hunting for prey, although I am not acquainted with any particular observations on the performance of such actions by them. On the other hand it may be objected that a large number of Selachians are as pelagic and active in their habits as any fishes, never use their snout for probing the ground, but pursue other active fishes in mid-water. This is true of the common spiny dog-fish, *Acanthias vulgaris*, and of the large species of *Carcharias* living in tropical seas. I cannot pretend to be able to explain all the difficulties presented by such species, but it is certainly a fact that there are among them differences in the degree of prolongation of the snout, and that when the mouth is nearer to the end of the head, the tail is more bent up so as to approach the homocercal condition. This correlation is evident enough in *Læmargus borealis*, the Greenland shark, and in *Selache maxima*, the basking shark. Concerning the aperticolous habits of the latter there can be no doubt, since it lives on plankton, while the Greenland shark has a great avidity for whale's flesh, and also devours fishes.

It is a remarkable fact that the most ancient Selachian forms of which anything like complete remains have been preserved do not resemble the recent forms in the characters of snout and tail. The mouth in them is terminal, and the tail either diphyccercal or nearly homocercal. In *Pleuracanthus* we find the former condition; in *Acanthodes*, the ventral lobe of the caudal fin is well developed while the upturned caudal extremity of the body is short, so that we have an approach to a secondary symmetry which in *Cladoselache* of the Lower Carboniferous becomes remarkably perfect, the dorsal and ventral lobes being equal, although the dorsal is still formed not by fin-rays but by the upturned extremity of the trunk.

Such facts as these strongly suggest that it is possible to over-estimate the importance of chronological position in interpreting the evolution of animal forms. Certain adaptations are found in unexpected perfection in geological periods which have been supposed to be characterised



by generalised forms corresponding to the diagrams of primitive ancestors invented by the ingenious morphologist. As we are forced to modify our earlier views by additional evidence we become more and more convinced that it is not length of time which is so important in organic evolution, *i.e.*, in the modification of structure, but change of the conditions of life. There can be no doubt that the heterocercal condition of the tail in fishes has been derived from the diphyrcercal, but the latter is scarcely less common at the present day than it was among the fishes of the Palæozoic age. In both cases it appears to exist in connection with certain habits, certain modes of swimming, which are not confined to one kind of habitat. Thus we find it in more or less perfect development in *Chlamydoselache*, which is a deep-water shark, in *Protopterus* which is a Dipnoan living in rivers, and the Ganoid *Polypterus*, likewise a fluviatile fish. In all these cases the movement of the fish seems to be rather slow, and horizontal in direction.

To return to the heterocercal tail. It exists both at the present day and in former periods, back to the Palæozoic, among the fishes now united under the name Teleostomes, formerly separated into the two divisions Ganoids and Teleosteans. Instead of these two divisions we have now the two sub-divisions Crossopterygians and Actinopterygians, distinguished by the structure of the paired fins, the former having fringed fins, the latter fan-shaped fins. The heterocercal tail is quite as exclusively characteristic of the Actinopterygians as the structure of their paired fins. Both types have persisted from the Palæozoic period to the present day, but the Teleosteans with homocercal tails are undoubtedly connected by a series of intermediate forms with the heterocercal Actinopterygians. The question then which we have to consider is whether there is evidence that the earlier heterocercal Actinopterygians sought their food upon the bottom.

In answer to this question we can say that fossil forms similar to the sturgeon are very ancient. In *Palæoniscus* the snout is slightly produced beyond the jaws but not so much as in the sturgeon. It is found in the Permian. But

in the majority of the Palæoniscidæ and Platysomidæ the mouth is terminal, and although the tail is heterocercal it approximates in most cases towards the homocercal condition in the fact that the ventral lobe is so large as to be equal or nearly equal to the dorsal lobe which contains the upturned extremity of the vertebral column.

In the Dapediidæ, Pycnodontidæ, Caturidæ and Lepidolepididæ, which are represented principally in Mesozoic strata, we have obviously the forerunners of the homocercal Teleosteans, and in them the homocercal condition of the tail practically complete.

If as I have suggested the benefit of the heterocercal tail lies in the effect it has of throwing the hinder end of the body upwards when it is moved, still the lateral motion of the tail could not give a stimulus to the hypertrophy of the ventral fin-rays. The origin of the modification must be sought in some particular stimulation of these rays. Such a stimulation might well be produced by the direct movement of the rays themselves. There is in fishes a movement of the rays by the muscles attached to them, in addition to the movement of the caudal region by the lateral trunk muscles. My theory therefore is that the development of the heterocercal tail from the diphyccercal was due to the concentration of active exertion in the ventral fin-rays, so that in course of generations these were hypertrophied and the others atrophied. The object of this exertion is assumed to be the raising of the tail and the depression of the head in fishes which fed upon the bottom. The lobe having once been hypertrophied the further modification in fishes which moved actively, even when they ceased to feed on the bottom, and swam chiefly in a horizontal direction, would take the form of a further modification in the shape and position of the ventral lobe until the homocercal condition was attained.

It is a remarkable fact that although the Pleuronectidæ and Gadidæ have generally been considered to be so similar that they have been placed in the same order Anacanthini, the structure and development of the tail described above occur in the flat fishes but are entirely



wanting in the Gadidæ. In the latter the tail is permanently diphycceral, it is composed of dorsal and ventral rays which are equal in number and size, and in fact closely resembles the tail of the extinct *Cœlacanthidæ*. There can be little doubt that even if the Gadidæ cannot be directly derived from the latter family they are descended from Crossopterygian Ganoids with diphyccercal tails, and have never passed through a heterocercal condition. Although the structure of the tail in the Gadidæ was briefly and correctly described by Alexander Agassiez in his paper on the "Development of the Tail," he did not attach sufficient importance to it, believing that a very slight apparent up-bending of the termination of the notochord showed the essential similarity in the development of this type of tail with that seen in other Teleosteans. The proper classification of the Anacanthini is yet to be worked out, but there can be no doubt that the Gadidæ and Pleuronectidæ, instead of being closely allied, are very remote from each other in structure and descent.

The recapitulative development of the tail in many Teleosteans by no means proves that the larval condition as a whole in those forms represents the condition of an adult ancestor. We do not find that the scales in development pass through an Elasmobranch and then a Ganoid stage. On the contrary, they are developed directly. There can be little doubt that the larvæ hatched from pelagic eggs, as well as the eggs themselves, are a direct adaptation to the conditions of life of marine fishes. It is not possible at present to say what are the conditions which tend to increase the number and diminish the size of eggs, but pelagic eggs are smaller and more numerous than those which are attached to solid objects in fresh water or in the littoral region. The pelagic larva presents many peculiarities which are obviously not ancestral, among them the fusion of the veins of the yolk-sac into one continuous chamber surrounding the yolk and communicating with a wide opening at the hinder end of the heart. This may be explained without difficulty on Lamarckian principles as the result of the small quantity of mesoblast available at the

very early stage in which the larva has to begin to obtain its food. The early use of the jaws, muscles, and sense-organs would cause their precocious development, so that the quantity of mesoblast surrounding the yolk-sac would be reduced, and thus the veins could no longer at this stage be divided from each other.

No Ichthyologist doubts that the fishes with closed air-bladders have been derived from forms in which the bladder opened from the gullet or other part of the intestines. The Physostomi retain other primitive characters besides the opening of the air-bladder, for example, the posterior position of the anus and of the pelvic fins. In the Anacanthini and Acanthopterygii the position of the anus is more anterior, and the pelvic fins instead of being placed in the hinder region of the body are, in most cases, either below or actually in front of the pectoral fins. According to the law of recapitulation we should expect to find that the larvæ of the two groups were similar in the position of the anus and the origin of the pelvic fins. But this is not the case. In the physostomous larva the anus is near the end of the tail, and separated by a considerable interval from the yolk-sac, while in the physoclist larva the rectum and anus are immediately behind the yolk-sac, and far in front of the end of the tail. The explanation here appears to be that in the adult the anus has been pushed forward by the increased use and consequent increased development of the ventral fin (so-called anal fin), and that the new condition is developed directly because there is no influence in larval life tending to retain the ancestral condition. The ontogeny of the pelvic fins in the Physoclisti is more recapitulative, but not completely so. The fins when they first appear are small dermal folds behind the pectoral fins, but they very soon pass to the position which they occupy in the adult. It is not very easy to discern the probable causes of the alteration in the position of the pelvic fins either on Darwinian or Lamarckian principles, but we may reasonably suppose that the particular position of these fins in the adult has been determined by certain requirements of attitude and movement in the fish. The mechanical conditions



of the movement of a fish in the water are not very definitely known. But the selectionist must assume that the position of the pelvic fins is a mechanical advantage, and if that is the case the change of position would necessarily be produced on Lamarckian principles by the directions in which the muscles were exerted.

Among particular cases of metamorphosis in fishes none is more remarkable or has attracted more attention than that of the flat-fishes. This has always been cited as a conspicuous case of recapitulation, as it certainly is. But it also illustrates very forcibly the principle here maintained, that recapitulation of modifications of structure depends not merely on heredity, but to a very important extent on recapitulation of changes of condition. The pelagic larva of *Pleuronectes*, *Solea* or *Rhombus* is very closely similar to that of the Gadidæ or of many Acanthopterygians. We may well believe that this pelagic larval condition had been acquired before the peculiar condition of the flat fishes had been evolved. The larval symmetrical condition represents therefore not the adult condition but the larval condition of the ancestor. New conditions of life and consequent modifications of structure have been introduced into the adult stage of life, while the conditions and the structure of the larva have remained unchanged. Whether the habit of lying on the bottom on one side was originally acquired at an early or a late age, it is certain that it has come to be assumed at a very early age, and consequently the structural changes which we know to be associated with it are now in great part simultaneous with the ordinary development of the adult structures of the fish. For this reason it is by no means easy to ascertain from the ontogeny of the flat fish, much as the process has been studied, the characters of the adult ancestors. The assumption of the special Pleuronectoid characters is most retarded in species of *Rhombus* and their allies, such as the turbot and brill. In these cases we find stages in which the eyes are still symmetrical when the fin-rays are well developed, and we see a symmetrical fish with a morphologically heterocercal tail, a single dorsal and a single ventral fin, neither extending so far forward as

in the adult flat fish, and dermal spines somewhere on the head. These dermal spines are additional evidence of the want of affinity between the Pleuronectidæ and Gadidæ. In searching for the possible ancestors of the flat fishes among extinct forms, we find the required characters most clearly represented in the Pycnodonts, a compact group which ranged from the Lias to the Eocene, in which latter formation fossil flat-fishes first appear. The Pycnodonts have a single dorsal and single anal fin, and each of these in some genera is much extended antero-posteriorly. The body also is compressed laterally and rhomboidal in shape. But it is doubtful whether the specialised dentition of the Pycnodonts could have given rise to the dentition of the Pleuronectidæ.

The precise nature of the changes which have taken place in the flat-fish in its modification from a symmetrical fish is as follows. The orbital region has been twisted so that the interorbital septum is brought round to the upper side, and the eye of the lower side to the upper. It cannot be said that we can point out with certainty the muscular efforts or mechanical strains which would produce changes in this direction in the individual as an acquired character. The action of the eye-muscles would probably have some effect, and the weight of the fish resting on the ground would force the lower eye-ball towards the upper side and so distort the face. In all probability both these influences have contributed to the result. If acquired characters are not inherited, at least evidence and logic force us, whether we will or not, to the conclusion that the modifications which have led to the condition of the eyes in flat fishes were determined by the mode of life which these fishes adopted. There is no evidence known to me which supports the view that such modifications, or variations which could lead by accumulation to such modifications, could possibly arise independently of the influence of external conditions.

Another modification which has occurred is the extension of both the dorsal and ventral fins in an anterior direction. The ventral fin is extended towards the head, pushing the anus before it, and passing ventral to the



viscera and abdominal cavity. The dorsal fin extends on to the head, its base being attached, not to the median line of the head, which is bent by the distortion of the eyes, but along the outer edge of the orbit belonging to the lower side, this edge being now in line with the dorsal edge of the body. This extension of the dorsal fin separates both eyes and orbits entirely from the lower side of the head, and adds greatly to the disguise beneath which the original symmetry of the fish is concealed. The increase in the extent of the median fins corresponds to the increased use which is made of them in the peculiar habits of the flat-fish. The lateral muscles of the body and tail are no longer constantly employed in locomotion, but the fish glides over the bottom by means of an undulating motion of its marginal fins. This motion involves the constant action of the numerous small muscles attached to the fin-rays. Such an action commencing in the individual at a period when the differentiation of the fin-rays from the embryonic tissue belonging to the fins was not completed, would tend it is believed to increase the development of such embryonic tissue and differentiate an increasing number of rays from it, while the direction of the muscular strains, the constant endeavour by muscular contraction to draw forward the anterior ends of the fins, would determine the direction of their extension. Thus the mode in which the fins were used would produce in the course of generations the structure and relations which they now possess.

The third chief general peculiarity of the flat-fishes is the absence of pigment from the skin of the lower side, an absence which has been shown by experiment to depend on the absence of light. It is a fact that pigment is developed on the lower side of these fishes when that side is exposed to light, and it is also a fact that when such exposure is maintained the lower side does not develop pigment so quickly or so abundantly as the upper side. It is maintained that the former fact proves that the character was originally acquired by the individual, the latter that it is now strongly inherited.

There are certain conditions of life which have produced

a similar effect on animals most remote from one another in structure and systematic position. Complete or nearly complete, and constant darkness is one of these conditions. Two modifications which are generally observed in animals living in darkness are diminution in the pigmentation of the skin and deterioration of the eyes. In most cases there is abundant evidence that the animals passing their lives in darkness have but recently diverged from forms which live in daylight. We may inquire then to what extent the ancestral condition is recapitulated in the ontogeny of these forms, with regard to the two adaptations mentioned. Not long ago this question was raised in a controversy concerning the possibility of explaining the loss of the eyes in cave-inhabiting animals by the selection of individual variations. Professor Lankester had suggested that the individuals which had the best eyes were better able to find their way out of the dark recesses into which they were accidentally carried, because they would detect a glimmer of light which those whose eyes were less perfect would not notice, and the former moving towards the source of the light would emerge into the open air again. It seemed to me that this hypothesis was contradicted by the fact of the recapitulation of the eyes, because when very young all the individuals are able to see, and would therefore all be able to escape in the manner suggested.

But we must turn to the results of direct observation in order to ascertain to what extent this is correct, whether the eyes are fully developed in the immature stages of cave animals which are blind when adult. Unfortunately observations on the ontogeny of such animals are by no means complete or detailed, but still enough has been ascertained to show that recapitulation is neither perfect nor altogether wanting.

*Troglocaris Schmidtii* is a crustacean of the caves of Europe, which is quite blind in the adult condition; it was found by Dr. Joseph that the embryo while still within the egg was provided with eyes.

In the adult *Proteus* of the caves of Adelsberg in Dalmatia, the eyes are very small and entirely covered by the



skin. But in the young when it is first hatched the eyes are well developed.

*Typhlogobius californiensis* is a species of Goby living on the shore near San Diego in California. It lives usually in the holes of a burrowing carideoid crustacean, and has aborted eyes and a pink colour. The whole frontal region of the skull of this fish is much modified, the scales have entirely disappeared, and the spinous dorsal fin has been much diminished in size. In a small specimen .9 in. long the eyes were visible and apparently functional, but in larger and adult specimens there is a thick layer of skin over the eyes so that the latter can scarcely be perceived, and certainly cannot enable the fish to see. The size of the eye was not however found to be obviously different in the smallest and largest specimens.

A detailed description of the minute structure of the eyes of this blind fish in the adult condition has been published by W. E. Ritter in America, but unfortunately he had no embryos or larval stages and therefore was unable to compare the condition of the eyes in the earlier and later stages of life or of the ontogeny. The smallest specimens examined were 19 mm. long or nearly  $\frac{4}{5}$  in. and the largest 63 mm. or nearly  $2\frac{3}{5}$  in. Comparison of the various specimens did not prove either a constant advance or a constant retrogression in the development of the eye between these sizes, but it is noteworthy that the only specimen in which the lens was entirely absent was one of the maximum size, 63 mm. in length. The usual condition of the eyes was the following. The epidermis over the eye is similar to the ordinary epidermis. Beneath this is dermal fibrous tissue also of the ordinary kind. Around the eye is a thin layer of denser tissue representing the sclerotic and cornea. The choroid is thin and rudimentary, in front of it is the pigment layer of the retina which is proportionally very thick and contains no cellular elements. In front of the pigmented layer is the cellular part of the retina which is but little differentiated; it contains however a layer of rods but no cones. The lens is present with the exception mentioned above, but the argentea is entirely absent, and

likewise the vitreous humour. Optic nerve and eye muscle are present but very slender and long.

In 1891 the eggs of this Goby were found attached to the lower side of the rocks beneath which the fish lives, and in the embryo before hatching the development of the eyes was found to be perfectly normal, and similar to that which takes place in other fish embryos.

In the eye of *Proteus* a progressive development of the lens in the embryo and its subsequent degeneration and total disappearance in the adult have been definitely observed by Schlamp (1892). It develops normally from the epiblast and sinks into the opening of the secondary optic vesicle where it is still to be found in the hatched larva. It does not advance however beyond the embryonic cellular structure, and in quite young animals is already much reduced in size; in the adult not a trace of it remains. The vitreous body is also absent in *Proteus*, the retina and optic nerve are present. The retina in consequence of the absence of the vitreous body does not spread out flat but forms a solid spherical mass whose histological structure is not markedly different from that of other Amphibia, but the terminal elements (rods and cones) do not reach their perfect form. In the Mole (*Talpa*) the lens is present though it retains its embryonic cellular structure throughout life, and in this respect is more rudimentary than the lens of *Typhlogobius*. The choroid is but slightly developed, and has little pigment, while the pigment layer of the retina is highly developed. The cellular layer of the retina is present but not fully differentiated; rods and cones according to Kohl are both present. The vitreous body is also present, and likewise the optic nerve, which Semper stated to degenerate in adult life.

Three species of blind crayfishes are known which inhabit subterranean waters in North America, in Missouri, Kentucky, and Tennessee. They are *Cambarus pellucidus*, Tellkamp; *C. hamulatus*, Cope and Packard; and *C. setosus*, Faxon. The eyes in these, to superficial observation, appear to be absent. The eye-stalks are present but they terminate in a blunt cone instead of a bulbous enlargement,



and no black pigment is visible at their extremities. Tellkamp as quoted by A. S. Packard in the *American Naturalist*, 1871, stated that the eyes were larger in the young of *C. pellucidus* than in the adult. Garman (1889) says that the eyes are more prominent in young specimens of *C. setosus*, and appear to lack but the pigment.

The minute structure of the eyes in the adult of *C. setosus* and *pellucidus* has been described in detail by G. H. Parker (1890), but I have not been able to discover that any investigation of the development or of the structure of the eyes in the embryos or young has yet been made. The optic stalks are not only pointed, but smaller than in eyed crayfishes. In *C. setosus* the end of the optic stalk is covered with an undifferentiated cuticle of uniform thickness, and similar to that of the rest of the body. No indication of the facets characteristic of functional eyes is present. The so-called hypodermis, the cellular layer beneath the cuticle, is also undifferentiated: the only feature in which the hypodermis of the retinal region differs from that of other regions is that it contains two or three irregular rows of nuclei instead of a single one. There is, however, below the hypodermis within the eye-stalk an optic ganglion of considerable size, and from this ganglion there passes a short narrow optic nerve which extends to the hypodermis. The complicated structure of the retina which exists in functional crustacean eyes has therefore completely degenerated, so that it has reverted to the condition of undifferentiated hypodermis. Pigment is entirely absent. The condition was observed in three specimens, two of which were 6 cm. long, the third 4.2 cm.

In *Cambarus pellucidus* the condition of the cuticle was the same, and the optic ganglion and nerve were present as in *setosus*, but the structure of the retinal region was different. Degeneration had not proceeded so far. The rudimentary retina connected with the optic nerve is thickened, forming a lens-shaped mass, which contains, besides nucleated cells like the ordinary hypodermis cells, large multinucleated granular bodies. Parker gives his reasons for considering these granular bodies as the de-

generate representatives of the groups of four cone cells each, which are present in normal retinulæ.

We have then in the case of the blind dwellers in darkness a physical condition which is uniform and constant throughout life, and a structural condition obviously related to it which is not direct but recapitulative in its development. The development of the eyes in these forms offers a marked contrast therefore to the entire absence of the forelimbs of snakes at all ages, and resembles the development of teeth in the gums of the foetal whale. The following conclusions follow necessarily from the facts.

(1) The blindness of cave animals has certainly not been produced by the selection or survival of individuals in which the eyes were defective from their first development. If it is due to selection at all, it is the selection of individuals in which the eyes underwent progressive deterioration after the commencement of independent life.

(2) The eyes even in the stage in which they are most developed are far from being as well developed as in the ancestors which lived in daylight, but are only somewhat more developed than in the adult animal. Recapitulation does not therefore occur except when the external condition to which the ancestral structure was adapted continues to act at an early period of life.

In this case, therefore, as in many others, if we persist in applying the selection theory of evolution we must be content to infer that the variations occurred in particular ways without any particular reason. If hereditary variations are independent of the external conditions of life there is no reason why the eyes of blind animals should be better developed in the young than in the adult. It cannot be maintained that this is due to a general law of inferior variations, that the absence of selection allowed individuals with inferior eyes to survive and breed, and that congenital inferiority of an organ always manifests itself by its degeneration at a late period of life. On the contrary we know plenty of cases in which an organ is absent in the young and fully developed in the adult. The facts compel us to conclude that the ontogeny of the individual has been



modified in correspondence with the uniformity or the periodicity of the external conditions to which it is exposed, and we can only infer that the influence of the external conditions is the cause of the modifications. We have reason to believe that in the individual the total absence of light leads to a progressive deterioration of eyes, and if this progressive change, repeated in every generation, ultimately becomes hereditary, then it would begin earlier and proceed farther in successive generations. On this view the very imperfect and incomplete recapitulation which we actually observe is the necessary consequence of the fact that the animals are exposed throughout their ontogeny to complete darkness.

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## SOME PHYSIOLOGICAL ASPECTS OF HYPNOTISM.<sup>1</sup>

MENTAL phenomena may be viewed from two entirely different standpoints. With one of these aspects, that furnished by the introspective method, a physiologist has no business to meddle, but the other, in which the Brain is considered as the organ of mind, forms a most important part of the Physiology of the Nervous System.

Mind is undoubtedly correlated with the existence of special living structures; the processes which constitute, in physiological parlance, the functional attributes of nervous tissues are transmuted in the crucible of consciousness into the various moods of sensation, thought and volition. The *rationale* of such transformation is as inexplicable as that of the origin of matter or the commencement of life.

From the physiologist's point of view, the transmutation is one in which material changes capable of investigation by physical methods are suddenly associated with the presence of immaterial phenomena, the characters of which his methods are impotent to decipher. He recognises that this condition which has suddenly burst into blossom is, from another point of view, existence itself, the conscious something provoked from senseless nothing, but, in spite of this recognition, he knows that the presence of the mental state

<sup>1</sup> A Lecture delivered at Magdalen College, Oxford, March, 1897.

is to be regarded by him merely as a sign indicative of the full development of those underlying physiological processes which are the object of his investigation.

The phenomena of Hypnotism may be viewed from such a standpoint, the mental conditions being used as signs of the development of physiological states. The subject is one of great interest to both physiologists and psychologists, since the curious phenomena of the hypnotic state appear to be focussed around two phases of mental mood which are themselves of fundamental importance, "attention" and "suggestion"—the first a predominant factor in determining intellectual growth, the second a determinant of the manifestation of volition. The profound modification which the cerebral activities undergo through the production of the hypnotic state brings these two aspects of mental conditions into special prominence, and thus the phenomena of hypnotism may not improbably provide a clue towards the better realisation of the presumed physiological processes which underlie these and other mental traits.

It must be confessed that our knowledge of such processes is most limited and vague, and that, as regards their fundamental nature, we are at present only able to make hypothetical inferences; still the inference, even if hypothetical, is strengthened by the circumstance that it is the transference to the highest portion of the nervous system of details more or less well grounded in connection with lower portions of this system, and it gains in consequence of its logical character, more than it loses by the hypothetical element involved in the transference.

A physiological aspect of Hypnotism must therefore involve the special group of phenomena as part of nervous phenomena in general, and the object of the present article to set forth the extent to which modern views as to nerve structure and nerve activity can be utilised for throwing light upon the special physiology now under consideration. At the outset it is necessary to clear the ground by stating, in a very general way, what physiological conditions are held by the writer to denote the presence or absence of volitional power; such a statement is convenient for the



handling of the subject, but it must not be taken as in any sense a definition of volition.

Sensation or muscular activity in some form are the only certain indications to us of central nervous activity. When a specific form of such muscular activity is always obtained in response to a perfectly definite mode of sensory stimulation, then voluntary power is held to be in abeyance; the absence of the power of modifying the muscular response to specific sensory stimulation thus becomes the important test for determining whether the animal experimented upon has or has not volitional power. However closely an animal's actions resemble those in which volition is an undoubted concomitant, they must, in the absence of such possible modification, be termed automatic. Volitional paralysis thus involves inability to modify the response to definite sensory stimulus, hence such paralysis may result in the display of automatic activity, and this plays a prominent part in the production of hypnotic phenomena.

With this prelude we may proceed to consider quite briefly, some of the chief characters of the phenomena and the means by which they may be produced.

If a faceted piece of glass, a crystal or some bright object is held a few feet from a person's eyes and slightly above their level, and visual attention concentrated upon the object, then, after a variable time, a change may take place in the gazer. The pupils instead of remaining constricted, as they do involuntarily when the eyes are focussed on near objects, gradually dilate. There comes a time when the eyes of the subject no longer change on the approach of the hands of the operator, when the closure of the eyelids by the operator is not followed by an effort to open them, when the subject is thus found to have, to a great extent, lost his voluntary power and to have relapsed into a condition which superficially resembles that of sleep.

This initial sleep of Hypnotism is, however, unlike ordinary sleep, for in the latter the whole nervous system is in a state of subdued activity (thus respiration is slow and shallow), but in the Hypnotic sleep the involuntary

movements determined by the lower portions of the nervous system are exaggerated. A large number of animals are susceptible to the production of this peculiar state.

As early as 1656 Kircher observed that a fowl held with its head on the table, so that the gaze should be fixed on a chalk line drawn in front of it, became motionless after a short time; he called this the *experimentum mirabile*. The humble frog if placed on its back and released, at once turns over into its normal position, but if kept on its back in such a way that all movements are gently suppressed with the head held rigid, it becomes after a few minutes motionless, and remains in this attitude for a little time, a hypnotised frog.

Rabbits, guinea pigs, birds and reptiles can all be brought into the same state by the use of similar methods. In a French poultry-yard refractory hens who persisted in sitting on addled eggs have been profoundly hypnotised by holding their heads under their wings; they have been then placed, when in the state of hypnotic sleep, on a new batch of sound eggs, and, what is more remarkable, have on being wakened at once accepted the responsibilities of the new situation.

The distinction between hypnotic and ordinary sleep is further accentuated by the circumstance that the former change is one which may develop into other striking manifestations of nervous activity. If the closed eyes of a guinea-pig, appropriately hypnotised, are opened and a bright light allowed to flash upon them, the animal does not necessarily wake up and behave like a reasonable guinea pig, instead of doing so it may become cataleptic; all the muscles suddenly stiffen, owing to an uncontrollable rush of energy from the abnormally excitable nervous system. Similar phases of hypnotic existence may occur in man; the resulting muscular contractions being so pronounced that the individual may lie stiff, with merely the head and feet on two chairs, not yielding even when the stoutest member of the audience at the hypnotic *séance* is called up, and seats himself, at the request of the operator, upon the hypnotic's abdomen.



It is interesting to note<sup>1</sup> that cataleptic reflexes can be produced in response to skin stimulation in un hypnotised animals after the separation of the portions of the brain above the cerebellum and spinal cord.

A predominant characteristic of both these phases of the hypnotic state is evidently the paralysis of volitional power, and, as the state progresses, this is succeeded by a remarkable augmentation of other nervous functions. If the eyes have been opened then all the nervous-avenues for the production of sense impressions are present and, in response to peripheral sensory stimulation the nervous mechanism may re-act as it does in the normal waking state, but with two striking differences ; first, the actions must follow the sensory impression, they cannot be modified by voluntary control, and any resulting movement of the subject is thus automatic ; secondly the sensory impressions adequate to evoke the actions may be far more delicate than those which, in the waking state, are necessary to produce either specific consciousness or the appropriate volitional movement which this consciousness ushers in. The subject does what he is commanded to do ; for the nerve processes aroused in ear and eye by the sound of the words, and the gestures of the operator dominate the whole brain machinery of the subject, and a throng of impulses pours out to the appropriate muscles, without the subject being conscious of any stage in the process. It may even happen that the subject does actually remain conscious but impotent ; powerless to modify the domincering activity of the nerve mechanism ; his actions thus remain automatic although consciousness is present. So, too, in ordinary sleep we may be conscious, for we may dream and often remember our dreams when we wake, and yet we have been powerless to control our actions or to modify the ideas called up by the nerve processes.

This stage, generally an unconscious one, has been termed the somnambulistic stage of hypnotism and is the most interesting for reasons which will appear later. There is however another stage which may be briefly referred to.

<sup>1</sup> Sherrington, *Proc. Roy. Soc.*, 1897 ; Horsley, *Proc. Roy. Soc.*, 1897.

The physiological derangement, which is the basis of the volitional abeyance and of the exalted nervous activities just described, may, if hypnotism is profound, pass into a more widespread derangement, exhibiting itself as deep hypnotic sleep. It is now associated not only with paralysis of will but with profound anæsthesia, and the subject gives all the physiological evidences of lowered vitality of the whole central nervous system. If the state is prolonged it may become dangerous to life by lowering the activities of those lower centres upon the vitality of which such essential processes as respiration, etc., depend. It may, for convenience, be distinguished as the condition of lethargy and resembles that produced by chloroform inhalation.

Proposals have been actually made to employ hypnotism as a method of producing anæsthesia. There are two grave objections to such employment. In order to produce a profound state of hypnotic lethargy, the subject must be made extremely susceptible, and this can only be brought about by repeated hypnotisation. Dr. Esdaile, who employed the method in India, found it necessary to hypnotise his patients every day for several weeks, before he could get them into a state of stupor sufficiently profound to enable him to operate with safety. It is scarcely necessary to point out how utterly unjustifiable such a procedure is; the state itself, when reached, is more dangerous to life than that produced by ether, and far more difficult to be recovered from, whilst, by the processes the subject has gone through, the patient has had those physiological activities upon which his volitional power depends excessively deranged and not improbably permanently enfeebled.

The states thus described—Hypnotic Sleep, Catalepsy, Somnambulism and Lethargy—are undoubtedly due to an abnormal condition of the physiological activities of the central nervous system. In order to suggest what, in accordance with modern physiology, may be presumed to be the *rationale* of this altered condition, it is necessary to sketch the essential features of normal nerve activity. This is correlated with the existence of specific structures and the possession by these of specific functional attributes.



In all higher animals, such as Vertebrates, the nervous system consists of peripheral nerves and central nervous substance, the latter being situated in the bony canal of the spinal column as the spinal cord, and in the skull as the cerebral hemispheres, cerebellum and medulla.

The central masses contain nerve-cells and their branches ; these branches may be short or long, some of the long branches form the essential vital portions of the nerves, the so-called nerve-fibres. There is no nerve-fibre which is not the process of a nerve-cell ; cut off from this the fibre becomes functionless. It further appears probable that no nerve-fibre is the branch of more than one nerve-cell ; each fibre by its course lays down an independent structural path, and although this may divide and subdivide indefinitely it remains distinct. Every nerve-cell with its branches thus forms a complete nervous microcosm, or, as far as the structural path it offers is concerned, a neuron. These may be said to be the two great discoveries of modern neurology, and it is in the light thrown by their realisation that physiological knowledge of the nervous system has to progress. A further fact, the discovery of which preceded those just referred to, is connected with the development of nerve. Nerve-fibres have grown from cells to or from muscles and sensory organs, and innumerable branches within the central nervous system have grown from the cells of one part to and near the cells of a more remote part, both in the spinal cord and the higher cerebral masses.

Sensory or up-lines of nerve communication thus exist from external sense organs to definite portions of the recipient masses ; motor or down lines from localised groups of cells in the central mass to muscular and other structures. Between the ends of the up lines in the central nervous mass and the commencement of the down lines in this mass, between the arrival and the departure platforms, is a gap unbridged by such nervous structures. The physiological peculiarities due to the existence of these gaps are those to which I especially desire to direct attention.

The more complex the central mass, the more tangled

becomes the skein of long cell processes (nerve-fibres), and of short cell processes; but, just as in the complicated woof of a great loom, so here, the nerve-fibres and short processes, constituting the living threads, remain distinct from each other though woven into close proximity.

Each up nerve-fibre entering the spinal cord divides into two, one branch descending ends near its entry, the other proceeds further to end in various regions nearer the cephalic portions of the system; some of these approach the start of one down line, some that of another, but the gaps always exist between the ending of the one and the commencement of any new line.

It is more difficult to describe, in general language which shall not be too technical, the essential features, not of nerve-structure but of nerve-activity.

The experimental study of the activity of isolated nervous structures has revealed three aspects of their vital phenomena, (1) Living nerves are in a molecular condition which is readily upset by a slight change in their surroundings; (2) they are so constituted that after such an upset they rapidly recover the old position of molecular equilibrium; (3) finally, the altered state due to the upset, although thus rapidly reconstituted, is passed on from the seats of disturbance to such neighbouring portions as lie in immediate structural and physiological continuity with the part that was originally upset. The first aspect, *i.e.*, the capacity to be thus upset is termed nerve-excitability; the second, the upset itself, the excitatory state; the third, the propagation of the upset, is termed nerve-transmission and such transmission constitutes what may, for brevity, be called the passage of a nervous impulse. This nervous impulse is thus compelled to travel along definite routes just as a flame is compelled to travel along a fuse, or a train along a railway line, and this is due to the fact that such travelling is the successive awakening of the line of communication, *i.e.* of portions of definite nerve-fibres. If now the long fuse or nerve-fibre is fired by a local change, in the latter case a change of a sensory end organ, and the nervous impulse thus started travels up the fibre, what may happen when it reaches such



central nervous masses as the spinal cord? The line here divides and the impulse thus scatters ; part may go on up to higher portions, but part may travel along the short processes until it reaches their terminations and arrives at the gaps. There it may end, since the line ends ; but it may force the gap, struggling through it. In doing this the most obvious fact is the extra time involved in such passage. An impulse takes only  $\frac{1}{100}$  sec. to travel up 12 inches of nerve-fibre, it takes, under the most favourable conditions, at least another  $\frac{1}{100}$  sec. to struggle across the microscopic gap. For this struggle it may be inadequate and be thus extinguished, but, if it succeeds and reaches the shore of the cell from which the down line starts then it travels rapidly along this to the muscles, and muscular movement must ensue. This is the physiological basis of reflex action indicated in its utmost simplicity and even the most complicated involuntary, that is automatic, movements must involve similar central physiological processes. Two further aspects of these processes remain to be referred to, since they form the basis of those conceptions of the physiological changes in the hypnotic state first put forward by Heidenhain and by Preyer. One of these aspects is associated with the distribution of the structural path ; on the ingoing or sensory side the lines divide many times and thus the ingoing impulse is conveyed to many regions ; it may thus struggle through gaps in many different situations, and emerge, along various outgoing motor lines, to widely separated organs. This is the physiological expression of the familiar experience that an ingoing nerve-impulse (such as that caused by a prick on the skin) can spread and emerge so as to produce movements of distinct groups of muscles, in arms, legs and larynx. The second aspect is due to the struggle necessary to force a passage through the gap ; the physiological path here offers a resistance, hence an ingoing impulse, if weak, may result in no obvious movement. Unable to force the gaps, it has been extinguished at the ends of the ingoing tracts ; it has perished in the attempt to cross this unknown region. When once such an impulse has struggled across the gap, nothing can stop its further pas-

sage along the new nerve path which it has entered. It travels along the line thus afforded until it reaches the next gap, when it has to struggle through this. What are the conditions which will be favourable to the forcing of gaps by such impulses? They may be described broadly as of two kinds. One set of conditions is obvious enough: it is associated with the intensity of the impulse itself; the way to produce reflex movements in response to nerve-stimulation is to have such stimulation strong enough. The other set of conditions is more subtle in its causation but equally simple to realise; it is the alteration in the resistance which the gap itself offers to the struggling impulse.

The whole of modern physiology is inexplicable, except on the supposition that the gaps are susceptible of alteration. What this alteration is we do not know; the gap consists of living tissue, and, like all living structures, is constantly undergoing molecular change. It is such ebb and flow which is the essential feature comprised by the term living. It is possible that the alteration is an actual approximation or separation of the terminal cell processes on each side of the gap. But although the nature of the molecular changes causing the alteration are at present doubtful, the physiological agencies by which this can be produced are more definitely known. The resistance of the gap is at the beck and call of nervous impulses proceeding to it along fibres from other portions of the whole nervous system. This is especially the case with nerve impulses which descend to the neighbourhood of the gap from the higher nerve centres. The arrival of such impulses may augment the stability of the molecular arrangements, increase the resistance and thus inhibit or check by this added resistance the passage of the gap by other nerve impulses. It has also been found that the arrival of nerve impulses along other lines or from other higher regions, may, but to a much less degree, decrease the resistance and thus augment the facilities for the passage. Such play, technically termed inhibition and augmentation, or reinforcement, is always going on; the higher centres are always discharging impulses which act in these two ways upon the lower, and the



summed effect is generally inhibition, *i.e.*, increased resistance of the lower gaps. The physiological proofs of this are numberless. I need only cite one: the reflex actions of such an animal as the frog are always aroused with far more ease if the higher centres are not present. The higher centres thus rein in the others, and by paralysing these the reins are cut, the resistance of the gaps is diminished, and they are rendered easier to force.

It is this last phase of central physiological activity which has been assumed by Heidenhain and others to come into play in Hypnotism, and to cause some of those profound alterations in the whole nervous system which are striking characteristics of hypnotic phenomena.

I have already pointed out that the simple method used to hypnotise in man is that of fixed gaze in a slightly strained attitude of vision, necessitating concentrated attention and a prolonged effort of the will. In animals the simple method is forced inactivity and uniform sense impression. A definite view as to the physiological basis of will is beyond modern physiology, but it has been already stated that physiologically it includes capacity to modify the paths of nervous impulses; and it appears probable therefore that the agencies affecting such modification are the play of other impulses upon the resistance of the gaps. It may further be stated that this is probably effected by a specific combination of co-ordinated impulses emerging from the highest parts of the nervous organism, the cerebral hemispheres. Some physiologists (Wundt,<sup>1</sup> for instance) localise these in one portion, the apperception centres of the Frontal Lobes. The process of forced and persistent attention demands continued play of this kind inhibiting some, augmenting other gap resistances in the brain and cord. Physiological investigation shows plainly that continued activity of nerve-fibres is not accompanied by deleterious changes in the nerve-fibres. These are indefatigable, but it is quite otherwise with the structures which surround the endings of nerve-fibres. Here continued activity is deleterious, producing increased resistance to the

<sup>1</sup> Wundt, *Hypnotisme et Suggestion*, 1893.

passage of impulses and the phenomena grouped under the term fatigue. In man the strained and persistent gaze of the subject may result in the production of such fatigue changes in those nerve-endings gaps, the forcing of which is a necessary concomitant of the mental mood of volitional attention; if these become paralysed the volitional power will be in abeyance, and the sleep of Hypnotism ensues. In animals a similar condition is brought about by the forced inactivity and persistent state of constraint. It is this phase of the physiological conditions which Preyer has laid stress upon. The *rationale* of the changes as described above may be considered fanciful by psychologists, but it appears, at any rate, that the resultant effect on the remaining portions of the nervous system is tolerably definite. The particular co-ordination of nervous processes which underlie volition have normally resulted in a varied discharge along nerve-paths to lower centres playing upon gaps, and on the cessation or diminution of such discharges, such regions are released from the inhibitory restraint thus imposed. The other nervous centres are now in a condition to respond with greater ease to the arrival of nervous impulses started in peripheral sense organs; in other words, the gaps are capable of being forced by impulses which would be inadequate were the voluntary power in full development. Such appears to be the condition of the nervous system in the somnambulistic state of hypnotisation with its unconsciousness, will-paralysis, and yet augmented capacity to respond to stimulation of the sense organs.

I am inclined to believe that the increased activity of all nervous processes, except those underlying volition, may be attributed to the diminished resistance of what are here termed the gaps. This itself may be produced, not only by the cessation of the inhibitory influences just described, but by the unrestrained and unmodified flow of such impulses as, by their play, directly diminish the gap-resistance, and thus augment the activity of lower centres. The cataleptic reflexes obtained in the monkey, etc., after removal of the cerebral hemispheres, are probably largely due to the operation of this second factor, which becomes



prominent owing to the cessation of the inhibitory influences. In popular language, the reins by means of which inhibitory restraint was possible having been cut, the influence of the whip has full play. In the case of the somnambulist, the resultant augmentation of nervous centres may be so pronounced as to outlast the state of hypnotic unconsciousness and obvious will-paralysis, so that the subject may show the increased susceptibility to respond to sensory stimuli, even when other evidence of the actual condition of hypnotisation has disappeared. The following experimental data are illustrations of this feature.

Acuteness of Hearing, as tested by Beaunis,<sup>1</sup> was found in several instances to be twice as great in the somnambulistic stage and, in some cases, to remain greater after recovery. The rapidity with which a prearranged movement could be accomplished, in response to a definite sensory stimulus, what is known as central reaction time, was found to be accelerated from 0·3 to 0·2 of a second for hearing and from 0·17 sec. to 0·14 sec. for touch.

I now pass to the final and most subtle aspect of hypnotic phenomena, the part taken in the production of all these phenomena by the train of mental changes known as suggestion. This is in the main a subject which must be dealt with on the psychological side, but its physiological aspects may be conceived along the following lines. We are aware that one idea suggests another and that volitional movements are the outcome of such suggested ideation. The physiological basis for this is decidedly obscure, but modern neurology has comparatively recently brought into prominence one feature which is pertinent to the present inquiry. Functional activity is undoubtedly associated with structural growth, functional inactivity with actual dwindling or atrophy. It is only in the last few years that this has been extended to the processes of the central nervous system. The passage of nervous impulses across gaps is the functional activity of the terminal nerve-fibre branches; if persistently repeated these branches may be conceived as being brought into conditions favourable for their growth,

<sup>1</sup> Beaunis, *Le Somnambulisme*.

tending to approach one another, thus diminishing the actual extent of the gap resistance. With opposite conditions of prolonged inactivity they may tend to recede from each other. Hence the repeated storming of the gaps by nervous impulses would diminish the extent of the gaps and thus facilitate passage across them, provided that such repeated storming is not so persistent as to cause the deleterious changes which constitute fatigue.

The result is that a nerve change of similar type to one which has previously occurred finds its easiest path if it runs along all the old lines; every repetition thus sets up further alterations in localities which are already the seat of similar changes. If the physiological changes involved in such transmission are transmuted into consciousness then ideation follows, but even in the absence of any such transmutation we must assume that a portion of the material basis of the ideation occurs. Such material basis of the idea, a given localised set of changes can obviously occur whether consciousness is present or not, with its entire complexus of discharging nerve impulses. Movements may thus be evoked of precisely similar character to those determined by volition, although both consciousness and volition are absent. Indeed, the absence of consciousness and volition, and the consequent exaltation of all other nervous activities causes such movements to be produced with greater promptitude and exactitude than would be the case if they were present, for now ideas and movements are constrained to follow a preceding set of the mental states. If consciousness is present we are aware of this sequential characteristic and we thus express it by the term "suggested". In the hypnotic state, "suggestion" is used to denote the same state of affairs, although both volition and consciousness are absent.

We are all aware that we fall an easy prey to such suggestion. "As iron sharpeneth iron so a man's countenance sharpeneth that of his friend." We are aware too that this influence is greater in proportion as volitional control and consciousness are in abeyance. How many of us, when changing our clothes in the middle of the day, and



thinking of something else, take out and involuntarily wind up our watches. The physician utilises this power of suggestion when he says to his patient, "You will be better soon". The reaction of the nervous system, in consequence of the suggestion, is one of the most potent of all remedies. But, in a hypnotised person, not only are consciousness and volitional power in abeyance, thus facilitating the sequence, but, in addition, the other nervous activities are augmented; hence we should expect that the power of suggestion would become extreme when by repeated subjection to the hypnotising processes the derangement of the system has become more and more marked.

Further, in such a deranged nervous system the installation of any one of the initial stages of the operations used to produce hypnotisation may obviously entail the whole sequence including even the will-paralysis.

In such people it becomes no longer necessary to fatigue the will by prolonged and concentrated attention in order to hypnotise; the operator may simply start the concentration by arresting the attention and then command the subject to fall into the hypnotic sleep. On the first trial the command will most undoubtedly be futile, but after a few experiences of the hypnotic state the will of many subjects does become paralysed on the word of command, on a gesture, on a look; with frequent repetition of the process, especially in highly sensitive neurotic individuals, a mere casual incident in the chain will arouse the state. The power of suggestion is so great that the Nancy school consider it the determining factor in the production of the Hypnotic state.

Examples are scarcely necessary, but I will refer here to one as illustrating a special point. A patient in the Salpêtrière used to be hypnotised at a certain hour. In her normal state she was allowed considerable freedom, and helped in the domestic duties of the establishment. One day she was discovered in a room having opened a chest and taken out some valuables that were not her own. During the theft the clock in the room had struck the hour at which she used to be hypnotised; with her nervous

system highly strung by the fear of detection, she fell a prey to the suggestion started by the sound of the clock and was hypnotised deeply, falling into the cataleptic state on the spot with the things in her hand, to be discovered red-handed some time afterwards, standing a stricken thief. Here it was not the word of command but an accidental accessory, a sensory impression, the potent feature of which was that it suggested hypnotisation because it was an immediate antecedent.

A subject may be thus hypnotised by a verbal command; a gesture, or a written line, even where this is to take effect the next day, or the next week; any one of these initial phases suggests the whole sequence. The hypnotisation of *Trilby* by the picture of Svengali, described in Du Maurier's novel, is founded on fact. Further the awakening may be achieved in a similar way by suggestion.<sup>1</sup>

It is no wonder, therefore, that such hypnotic subjects should readily respond to sensory impressions, even though these may be far too slight to awaken consciousness in the volitional onlooker. The unconscious subject is an exquisitely sensitive machine with a nervous system tuned to react to impressions of peripheral sense organs, which, acting on the ordinary volitional mortal, awaken no consciousness, and what is more they probably never can awaken the consciousness of such a normal individual since unconsciousness and volitional paralysis are essential factors in making the nervous machinery sufficiently sensitive to respond to the feeble stimuli.

Let me give some instances of such exquisite sensibility, choosing cases in which the series has been started by excessively minute impressions in peripheral sense organs.

1. *From the Skin*.—A hypnotised subject in a dark room is presented with a blank card from a whole series of fifty-two similar ones and allowed to poise it in the hand;

<sup>1</sup> This appears to me to be the answer to such critics of the physiological theories of Heidenhain and Preyer as Moll. His remark that the termination of Hypnosis by suggestion is not consistent with Preyer's fatigue theory of onset is in reality a statement that "suggestion" is inexplicable on this theory.



the card is taken away noted and returned to the pack and the subject being given the whole series, is commanded to choose this special card. The subject selected the card, saying she knew it by its feel and weight.

2. *From the Ear*.—A hypnotised subject was commanded to say when, among several men, a man with a watch entered the next room : the subject did so, saying suddenly that she heard the ticking of the watch in the man's pocket through the wall.

In both these cases there was a possibility of a sense-organ stimulus. The cards were not of equal weight and consistence and the inequality affected the skin of all, but the nervous impulses only forced a passage through the central nervous system of one—that of the hypnotised subject. The sound of the watch ticking must have really affected the ears of all, but the impression was so slight that only the brain of the hypnotised subject responded adequately to it.

3. *Sight*.—Instances of sight are innumerable. A sensitive subject, on being commanded to do so, was able to discriminate with the unassisted eye the details of histological preparations which, under ordinary circumstances, could only be ascertained by the use of a microscope, and to read print, the letters of which were only  $\frac{1}{250}$  of an inch long.<sup>1</sup>

The above instances are given as extreme cases illustrative of a very large number of analogous observations, and I refer to them in order to point out to those sceptics who, priding themselves on their common sense, are inclined to scoff, that there is no physiological reason for incredulity, although I fully admit there may be other grounds for suspecting fraud and trickery. The physiological essentials are an exquisitely sensitive nervous mechanism and a distinct initial sensory stimulus ; given these two, it is possible, and on the whole probable, that a true physiological sequence should ensue of the same character as that which would be produced by the same stimulus, if it were more pronounced but acting upon a less susceptible machine.

<sup>1</sup> Moll, *Hypnotism*, p. 101.

There is always one feature which is in favour of the truth of these observations; they have been observed in very sensitive somnambulistic subjects; that is to say, the recognition is achieved by people whose nervous system, through the frequent will-paralysis of hypnotism, is precisely in the condition in which it is able to respond to stimuli, which in ordinary life would be quite ineffectual.

The clairvoyant marvels of hypnotic *séances*, telling the number of a bank-note which an operator reads and puts in his waistcoat pocket, and other things of this kind, may, in many cases, possibly in all, be due to collusion and fraud, but there is no absolute physiological reason why they should be. Any person in the presence of such a hypnotised subject is really placed before an exquisitely sensitive machine which can respond to changes in his face, hands, eyes and voice, too small to be noted by either himself or any conscious bystander; it is certain that if such small changes occur they must produce physical phenomena of light, sound, etc.; it is certain that these must stream into and play upon the sense-organs; it is probable, there is no physiological reason against it, that the peripheral sense-organs may be in such a state of poise that they respond to these stimuli even though exquisitely minute, and it is not impossible that, if the terminal organs in eye, ear and skin do respond, the minute messages sent to the brain may produce the same effects as they would do if the person were in ordinary life, and the impulses were the same but much stronger. Further, every investigator may himself, by changes of which he is unconscious, suggest, and suggest unconsciously, to the hypnotised subject an idea which he has in his mind through such agencies as the muscles of expression, etc. The possibilities of suggestion are so extensive that it would be rash to fix a limit to them.

A great gulf, however, exists between all such responses to sensory stimulation, which, however improbable, are physiologically possible, and the doings of the *clairvoyante* who professes to tell not merely a past, but a present which cannot be known by the bystanders, which is happening the other side of the world, or outside the



material world altogether; who holds conversations with disembodied spirits, and is daring enough to project himself into a future which is, from the nature of things, non-existent. There is no known physiological basis even for telepathy, apart from sense-organ impressions, and *ex fortiori* none for such phenomena as the above. It may be that the nervous system will be subsequently found to react to physical changes in the surroundings which are at present unknown, but it is inconceivable that it should do so without such reaction being a response to a definite stimulus.

To a physiologist, with all the details of his science fresh in his mind, every response to an external stimulating agency must be one which involves a peripheral sense-organ and its afferent nerves. If telepathy cannot be explained by means of existing sense-organs, but demands a new sense, then the discovery of such a new sense-organ would alone furnish an adequate physiological basis. To suppose that the processes in one brain can, by a process akin to electrical induction, evoke analogous states in the brain of a distant separate individual is a supposition so opposed to the whole of physiological science as at present constituted that its conceivability demands a mental somersault on the part of the physiologist.

A great gulf thus divides the phenomena due to suggestion from those which are held by superficial observers to be of the same class, but which are in reality widely different, and the evidence for which, is so bound up with cases of imposture and fraud, as to be, in my opinion, unreliable.

I have endeavoured to show that the inhibition theory of Heidenhain and the fatigue theory of Preyer may be extended in the light of modern neurology so as to comprise the phenomena due to suggestion, and thus to afford a physiological hypothesis of the main features of hypnotic phenomena. In this endeavour special stress has been laid upon the part played by the little known substance which intervenes between the terminal processes of different nerve cells. It is not too much to say that the more precise

investigation of the structure and functions of these gaps situated around the termini of cell processes, will form one of the most important of the physiological inquiries of the next decade. Such investigation may be expected to throw a new light upon reflex phenomena, and inferentially upon the states of hypnosis ; the object of the present review of the subject is to indicate in popular language the extent to which the physiology of these gaps may be regarded as a determining factor of the essential characteristics of such modes of central nervous activity.

FRANCIS GOTCH.



## ARTIFICIAL FLIGHT.

I N a year when specialists in most branches of science are reviewing with jubilation the vast advances which have taken place in every subject of research during the Queen's reign, it is fitting that attention should be turned to the many, and often heroic, attempts that have been made in that period to obtain the mastery, for purposes of locomotion, of that most fickle of all elements, the atmosphere. It is true that hitherto these attempts have not succeeded in solving the problem of artificial flight, but progress in scientific investigation must not be estimated by the actual results achieved, and when the peculiar difficulties of the problem are taken into account, aeronauts will have every reason to be satisfied with the large amount of ground that has been covered during the past sixty years in bringing them nearer to the goal of their ambitions.

A record of the past history of artificial flight takes us back to the legend of Dædalus who as the inventor of sailing ships was not unnaturally accredited with having attached wings to himself. In the fourteenth century, J. B. Dante, a mathematician of Perugia is said to have crossed Lake Trasimene on wings, but further experiments resulted in his breaking a leg. In 1500 Leonardo da Vinci is said to have made some ingenious experiments on flight, and in the seventeenth century a romance was written by one Retif de la Bretonne describing the voyage of a flying man of whom a highly grotesque illustration was given. Passing from fiction to fact, we find in 1678 a French locksmith named Besnier experimenting with a system of double wings, so contrived as to close when raised and to open when depressed.

Besnier made a few experiments ; he first jumped off a stool, then he jumped off a table, then he jumped out of a window, and finally he actually succeeded in jumping off the top of a barn ; and the *Journal des Savants* tells us that his experiments met with *relative* success (*succès relatif*).

Subsequently he sold the machine to an acrobat, who used it for exhibiting purposes with success.

In 1709, Barthelemy Lourenço, a Portuguese, designed a flying machine, of which illustrations occur in old books. In appearance it was somewhat bird-like, and at either end were two spheres supposed to contain some sort of magic substance, probably either electricity or magnetism, which he imagined endowed with the power of lifting the machine into the air. In addition to these spheres there were a large number of funnels hanging from the top, which upon a windy day would conduct the wind to the under side of an awning and make it act as a sail. If the wind was not blowing, you used a pair of bellows instead, and a man is represented doing this in the figures given in old books. Barthelemy Lourenço wrote to the King of Portugal and submitted the design, asking the King to grant him the sole monopoly of making the machine. The King of Portugal replied that the request was far too modest, and that, in consideration of this wonderful discovery, he appointed Lourenço Professor of Mathematics at the University of Coimbra, at a salary of £3750 a year in French gold. In spite of the royal decree, however, the machine was, of course, never constructed.

An attempt was made in 1742, by the Marquis de Bacqueville to cross the Seine with wings, but unfortunately he broke his leg in addition, and the *Histoire des Ballons* relates that the experiment produced no further results.

Up to this point, it will be noticed, all attempts at aerial navigation had led to negative results. A great advance was made in 1783 by Montgolfier's discovery of the balloon, which opened up a new and highly promising field for research. Henceforth, aeronauts in France became divided into two sections, the *plus léger* party who sought to navigate the air by balloons, and the *plus lourd* who endeavoured to construct a machine which though heavier than air would lift itself after the manner of birds and flying animals. It was natural that the *plus léger* party should for many years hold the field, and we find from the close of



the last century up to the commencement of the Victorian era that balloons occupied a large share of public attention, not only in this country but still more so in France. Many balloonists made large fortunes in those days, and innumerable impossible schemes and fantastic devices were designed to gull the public; among these one of the most grotesque was an aerial vessel called the *Minerva*, with which Robertson proposed to make a tour of the world. The figure given in *Astra Castra* represents a globular balloon surmounted by a gigantic model of a cock bird, and suspended from it was to be a ship in case the balloon should come to grief and the party should have to sail across the sea. Attached by ropes below the ship was an enormous barrel containing provisions for the voyage, and near by a little house was suspended like a bird-cage for any ladies who might wish to accompany the expedition. Quite recently, we believe that a similar project of a balloon carrying a ship for use in emergency has been propounded in an American newspaper.

The earliest convert from the *plus lourde* to the *plus léger* school was the well-known aeronaut Blanchard, who shortly before Montgolfier's discovery had designed a most grotesque flying machine. The aeronaut sat in a chair and by working levers with his arms and legs raised and lowered four large paddles which were supposed to lift the machine. M. Tissandier's quaint figure of the machine is embellished by the addition of a small boy in the stern of the machine blowing a trumpet. The apparatus was designed, but Blanchard expected to get too little recompense for his experiments, and he was going to leave the country when the Abbé Devrunay kept him back and recommended him to take to balloons, which accordingly he did with success. Later on, one Austrian named Jacob Deeghen made a few experiments with a kind of double parachute, which he attempted to work up and down for the purpose of raising himself in the air; but he found that it would not quite lift his weight, so he attached it to a balloon and thus practically joined the ranks of the *plus léger* party. Deeghen took the parachute to Paris and was to have exhibited it there, but

when the French discovered that he was an Austrian they tore his machine to pieces—he himself only escaping after a thrashing.

The difficulty of controlling balloons has from the outset been recognised as the chief obstacle in the way of their adoption as means of locomotion. In the *Histoire des Ballons*, M. Tissandier reproduces an amusing eighteenth century cartoon published in France when ballooning was at its height, representing a *Méthode infaillible de diriger les Ballons*. The figure shows a balloon drawn along by donkeys, the man on the balloon is suspended by his waist and is blowing a horn and carrying a lantern to signal to the donkey-drivers.

In 1850 M. Pétin designed a great air-ship, and actually succeeded in raising over £1000 for its construction. The machine was to be supported by five balloons placed side by side and driven by a gigantic screw propeller. One of the weak points in his scheme was that Pétin said very little about the motive power. His figure, however, shows an engine rather resembling a traction engine at one side of the platform, which would be, one would think, rather a heavy load for the balloons and likely to disturb the balance of the machine. The machine was built, but before Pétin could make an ascent in France he quarrelled with certain officials, and the Prefect refused to give him the necessary permission. Accordingly he went over to England, and then to America, where he had another machine constructed, and made preparations to let it off at New Orleans. The machine was all ready, but it was found that the gasworks were not equal to the occasion, or, at any rate, this was Pétin's excuse for not going up.

Since the time of Pétin the problem of the navigable balloon has been attacked more or less continuously, sometimes, but rarely, with partial success. Among the earlier attempts, a kind of aerial machine was proposed by Lanson, who made experiments with it, but the results were far from conclusive. A system of steering a balloon, invented by M. Hellé, was never experimented with. Another navigable balloon was constructed by M. Dupuy de Lôme,



but the experiments made during the Franco-Prussian war did not lead to any result. Of a fourth contrivance a model was made by M. Julien, who exhibited it at the Hippodrome; it was a small model and would not work. That did not prove M. Julien to be wrong, because the model was on too small a scale to give a fair chance of success. If it had been made sufficiently large it would have worked satisfactorily, so the inventor said.

These old designs appear to us as absurd and grotesque; but Robertson's *Minerva* still survives in various forms, and M. Pétin has his counterpart in the many promoters of syndicates who even now from time to time issue prospectuses of air-ships with first and second class cabins, captain's rooms, engine rooms and saloons.

It is not much more than a year ago that the prospectus of a bicycle company was adorned with a picture of a man in mid-air on a bicycle, quite as fantastic as any of the illustrations in MM. Sircos and Pallier's work, or in *Astra Castra*, and a Toronto newspaper lately gave an extraordinary figure of the "Cowdon Air Navigating Machine" representing a kind of tramcar surmounted by three cigar-shaped tubes bearing the direction "Washington to New York," which tubes, the inventor imagined, or tried to make others imagine, would lift the car. In viewing such designs as these with the cool calculating eye of science, it will be found convenient for the purpose of a rough and ready test, to notice that air is rather over one-thousandth of the density of water, and the weight of the gas contained in a balloon, being somewhere about one-fifteenth of that of the air displaced as relatively small. It follows that a balloon will only support in round figures one-thousandth of the weight that would be supported by a ship of the same displacement. It is thus easy to sift out many worthless designs by imagining the gas bag to be reduced to one-tenth of its linear dimensions and immersed in water; in most cases it will be obvious that such a vessel would be utterly inadequate to support the weight of the machine. Another equally useful test is afforded by remembering that balloons will support about one ounce for every cubic

foot of displacement ; in face of which simple fact we find an inventor named Pennington only quite lately patenting a device for seats in an aerial car containing small cavities filled with gas, for the purpose of helping to raise the weight of the passengers, and we have been informed that he, like M. Pétin, has endeavoured to raise money for floating a company to work the scheme.

Continuing our historical retrospect, we learn that in 1854 Captain Le Bris made experiments with a sailing machine which he called an "artificial albatross," and which he released from the top of a cart. Partial success was accomplished, the machine at one time going 600 feet in distance in the air, but the experiments had to be discontinued for want of funds, not, however, till after Le Bris had broken his leg in an accident with the machine. In 1866 there was founded a new society "for the advancement of Aerial Navigation and for observations in Aerology connected therewith". Of this Society, which afterwards became the Aeronautical Society of Great Britain, the first President was the Duke of Argyll, and Mr. F. W. Brearey occupied the post of Honorary Secretary till his death in 1896. In 1868 the Society organised an exhibition at the Crystal Palace, commencing on 25th June. The light motor engines were probably the most important feature, and a prize of £100 was awarded to Mr. Stringfellow, whose steam engine, only weighing thirteen pounds with boiler, gave rather more than one horse-power. About the year 1870 De Villeneuve is reported to have constructed a flying machine driven by steam supplied from a fixed boiler through a flexible hose. On attaching himself to the apparatus and turning the steam on, De Villeneuve, to his surprise, was lifted off the ground, whereupon he stopped the engine in his alarm at the unexpected success of the experiment. In 1871 some experiments on air-resistance were conducted by the Aeronautical Society, a powerful current of air driven through a tube being employed. From that time on, till a few years ago, but few advances have been made, and aerial navigation seems to have undergone a dormant period ; the most noteworthy exception being the achieve-



ment of Messrs. Renaud and Krebs of the French war department, who in 1885 constructed a war balloon called "La France," capable of propulsion at a speed of about fourteen miles an hour. Unfortunately, in order to stem most of the winds that blow, a balloon would have to be driven at some forty miles an hour, and herein lies the the great difficulty which has prevented the *plus leger* party from making any great advances. Last year, however, Dr. Wölfert's steerable balloon was shown in working order at the Berlin Industrial Exhibition, and should have given satisfactory results. The gas bag was of oval shape, nearly 100 feet long and 30 feet in diameter, and there were two propellers, one about 9 feet in diameter in front of the car acting horizontally, and another placed underneath to raise and lower the machine. These propellers were to be driven by an eight horse-power<sup>1</sup> benzine engine making 500 revolutions per minute. Unfortunately, at a trial trip on 12th June, the baloon exploded and burst into flames, and both Dr. Wölfert and his assistant were killed.

A new era was opened by the *renaissance* of the *plus lourd* party which took place about the year 1891, with the advent of an army of workers, including the names of Maxim, Lilienthal, Langley, Pilcher, Chanute, Baden-Powell, Phillips and others. All these are now familiar names, and their apparatus and experiments have been so widely figured and described by the Press that a mere description of them here would hardly be of interest. To understand their true significance, however, it is necessary to consider one by one the various qualifications which are required to make up a successful flying machine, and how they have been attained.

The problem of artificial flight will practically be solved when a machine has been built which will raise itself and a man off the ground into free air, which can be propelled and guided for a certain distance in any desired direction, even against a moderate wind, without fear of its breaking or overturning, and which, with the experimenter, can be

<sup>1</sup> *Aeronautical Journal*, January, 1891.

brought safely to rest on the ground at the termination of the flight. The principal requisites are :—

- (i.) A sufficiently powerful and light motor.
- (ii.) Propellers, and aeroplanes of sufficient lifting power.
- (iii.) Balance and stability.
- (iv.) Appliances for steering and controlling the machine.
- (v.) Strength and rigidity.
- (vi.) Means of landing safely.

(i.) *The motor*.—The difficulties of flight at the beginning of the Queen's reign were entirely different to and far more insuperable than those of to-day. Up till quite recently no experiments on artificial flight could possibly have led to any practical successes owing to the want of light powerful engines or motors. The great advance made in late years in this direction, and which may be expected to be followed by further and greater advances in connection with autocars, has already entirely modified the conditions of the problem, and will probably continue to modify them still further in the future.

The early experimenters had no motive power to depend on beyond that of their own muscles, and we now know that man does not possess sufficient power in proportion to his weight to maintain himself in the air. He can start from the top of a hill and sail downwards through the air under gravity, and his rate of descent furnishes a simple if not quite accurate test of the power he would have to exert in order to fly. For if, instead of sailing in a downward path, a man wanted to fly horizontally, *he would require to exert about as much horse-power as would enable him to run up the hill carrying the flying machine with him, in the time that the flying machine takes to descend to the bottom.* Now Mr. Pilcher finds his rate of descent to be about five feet per second under favourable circumstances, and hence it follows that a two horse-power engine would be necessary to keep him afloat.

In discussing this point further, I cannot do better than quote from the data collected by Mr. Jeremiah Head in his



able address to the British Association at Nottingham. Dr. Haughton reckons that men rowing in a boat race exert about one quarter of a horse-power, and if we take a man weighing about twelve stone or 168 pounds, it follows that he weighs 672 pounds per horse-power that he is able to exert. Mr. Maxim, on the other hand, has proved that heavy birds only weigh 150 pounds per horse-power that they are capable of exerting; so that they possess about four times the horse-power per pound that we have. The albatross and the vulture probably go up to 250 pounds per horse-power. It thus appears impossible for man to fly by his own exertions.

But we are now able to construct machines which will develop a far greater horse-power in proportion to their weight than any bird. Ten years ago Mr. Thornycroft built a large torpedo-boat (the *Ariete*) which exerted one horse-power for every 191 pounds dead weight. This is less weight per horse-power than some birds possess; but we are not justified in concluding that the vessel could fly if it were furnished with wings, for horse-power per pound or weight per horse-power is not the *only* factor on which the possibility of flight depends. It does not follow that when the size of a bird or of a flying machine is increased the horse-power is directly proportional to the weight. That law of proportionality in fact we know fairly well does not hold. The horse-power must in fact increase more rapidly than it would do if merely proportional to the weight. Assuming that the resistance of the air is proportional to the superficial area and to the square of the velocity, and that flying animals of different sizes are similarly proportioned, according to M. de Lucy's law (which is roughly verified for birds and insects), a very simple piece of calculation by elementary mechanics will show that if all the dimensions of such an animal were quadrupled it would have to exert double the horse-power per pound, or 128 times the actual total horse-power, to sustain itself in flight. Under similar assumptions large flying machines would require greater horse-power per pound than small ones, the general law being that the horse-power per pound is propor-

tional to the square root of the linear dimensions. If, then, a large machine can be made to lift itself off the ground, a smaller machine could be more readily made to do so, and this circumstance adds weight to the experiments conducted on a large scale which have brought Mr. Hiram S. Maxim into prominence as an authority on aeronautical matters.

Maxim used steam power, the fuel used in the furnace being naphtha. This was burned in a very large number of burners (700 or more), so arranged as to give the largest possible area of flame. The steam was generated in a water-tube boiler similar to those now used on fast ships. It consisted of an enormously large number of fine tubes, giving the largest production of steam in the smallest space, while as for the engines they were so light that Maxim easily lifted them in his hands. The total weight of his machine was about 8000 pounds, and he reckoned that it did not weigh more than eleven pounds per horse-power. Seeing that birds may weigh 150 to 200 pounds per horse-power, it will be admitted that Maxim had sufficient motive power in proportion to weight; and, what is more conclusive, he has actually been able to make his machine lift itself from the ground when travelling at about thirty-seven miles an hour.

In order that there might be no danger of accident it ran on a railway, and outside there was an outer railway, so that as soon as it rose a few inches from the ground it pressed upwards on the outer rails, and should thus have been prevented from becoming uncontrollable. Once, however, when the engine was developing 362 horse-power, the outer rails gave way, and the machine actually did fly. That flight was a very expensive one, as it cost nearly £1000 to repair the machine, but from a scientific point of view it formed the crowning point of Maxim's experiments; for after the accident the rails were all torn up, affording proof positive that the machine possessed sufficient power in proportion to its weight not only to lift it into the air, but to bend the bars by which the outer wheels were attached, and to pull up the rails as well.

Of course, on the other hand, the construction of an



engine weighing eleven pounds per horse-power is a different matter to the construction of a one-horse-power engine weighing eleven pounds ; and as the primary object of all experiments is to obtain a machine that will carry the weight of a man, there are certain limits of size below which machines would not be of practical use. It may be noted, too, that the *steam turbine*, owing to its absence of vibration, promises to be a very useful and suitable motor for the purposes now considered, and may in all likelihood supersede engines with reciprocating parts.

(ii.) *Propellers and aeroplanes*.—Flight like all other forms of locomotion depends on the principle of action and reaction, but there is this important difference, that whereas in a rowing boat the reaction of the water on the blades of the oar only has to move the boat forward, in a bird or flying machine the reaction of the air set in motion by the wings or aeroplane has to continually overcome gravity. To keep a body heavier than air afloat in the atmosphere it is necessary that downward momentum should be continually communicated to the surrounding air at a rate proportional to and measured by the weight of the body. This communication of momentum involves the continuous expenditure of work, but this work is measured by the kinetic energy and not the momentum imparted to the air. This kinetic energy for given momentum is inversely proportional to the mass of air acted on, hence in order that there may be as little waste of power as possible in supporting an aerial machine it must be provided with aeroplanes acting on as large a mass of air as possible. Now there are two ways of acting on a great mass of air ; one is by constructing enormously large aeroplanes, the other is by imparting a considerable horizontal motion to the planes. For if we move a plane rapidly through the air in a horizontal direction it will constantly come in contact with fresh particles of air in succession, and it will thus be supported by a far larger mass of air than it would if it were to constantly remain in the same place, simply on account of the rate at which it moves. This property is not unknown to engineers ; the ordinary screw propeller of a ship affords another illus-

tration. If a ship is at rest in port and the screw is set in motion, very slight force is sufficient to keep the ship from moving, for the screw only keeps churning the same portions of water, and so has little power ; but as soon as the ship is under way the propeller is continually brought into contact with fresh portions of water previously at rest, and so gets a much greater grip on the water than when the ship was at rest in the harbour. But for this property it would be impossible to drive large ships forward with such small propellers as are commonly used. And just the same applies to aeroplanes.

These simple conclusions from elementary principles were verified in a striking manner by Professor Langley and Mr. Maxim, and the former has embodied the results of a long series of observations in his *Experiments on Aerodynamics*, which is now regarded as a standard work of reference. Mr. Maxim made similar investigations quite independently at the same time, a whirling table being used by both observers. The method was this : a plane was made to revolve round a central axis and the force of pressure of the air on it carefully measured so as to discover the laws according to which the resistance of the air varied when the velocity or the inclination of the plane was varied.

The first conclusion that these experiments brought out was that if a plane be held perfectly horizontally it falls to the ground less quickly if it has a horizontal motion imparted to it (as when made to travel round and round by means of this whirling table) than it would do if it were simply falling vertically. In other words, the horizontal velocity lengthens the time of falling. The curves obtained indicate that for small speeds the effect is not very great, but for speeds exceeding about thirty miles an hour the lengthening of the time of fall increases very rapidly.

The dropping plane, it will be seen, imparts a little downward motion to the air as it drops, but as soon as it has gone a little distance it comes in contact with fresh particles of air at rest ; it is never supported for any length of time by particles to which it has already imparted a per-



ceptible downward velocity; it is, therefore, constantly striking air *at rest*, and accordingly is much more retarded than it would be by making its way constantly through the air that it has set in motion.

The second result which Professor Langley and Mr. Maxim's experiments proved was this: the horse-power required to sustain a given weight in horizontal flight by means of an aeroplane of given dimensions is less for high speeds than for low ones. In other words, the faster the aeroplane travels, the less energy is required to keep it up in the air for the *same* length of time. This fact doubtless accounts for the high speeds at which birds fly, and it depends upon the same principle as the first result, namely, that the more rapidly the plane moves, the more it comes into contact with fresh particles of air at rest.

As regards the variation of the air pressure according to the inclination of the plane the general result of Professor Langley's observations was to confirm the empirical formula previously enunciated by Duchemin.

From the experiments of Professor Langley, it also appears that a rectangular aeroplane moving perpendicularly to its longest side experiences greater support from the air than it would do if it were moving in a direction parallel to its longest side. A flying machine should therefore imitate the shape of a bird—with narrow wings standing out at right angles to the direction of motion rather than that of a fish. This result is easily explained on the theory that in a wide plane the particles of air coming in contact with the hinder portion have already been set in motion by the foremost portion, and consequently less reaction can be obtained from them. A further verification of this explanation is afforded by Professor Langley's observations of the position of the centre of pressure, which in all cases is in front of the middle point of the rectangle, showing that the pressure is greatest on the foremost portions.

The advantages of narrow over wide planes have been most conclusively shown by Mr. Horatio Phillips in some experiments conducted at Wealdstone near Harrow a couple of years ago. "Phillips's Flying Machine," as it

was called, resembled a Venetian blind in structure, being constructed of a number of laths at a small distance one above the other and driven by an engine working a propeller. Although the machine was never allowed to fly, being constantly held attached to a whirling table, it rose from the little circular track on which it ran, and the lifting power of the planes was found to be considerably greater than that of a single wide plane of the same area. Phillips had made elaborate experiments on wide planes before coming to his present conclusions.

Although there are some difficulties in adopting the Venetian blind form to "soaring" experiments, the advantages arising from the use of narrow superposed planes are generally admitted by engineers, and they have been introduced in modified forms with considerable success.

Where however the wing surface is required to be of any considerable width from back to front, curved surfaces are better than plane ones, as I now hope to explain.

When an inclined plane surface is moving in a horizontal direction or is acted on by a horizontal wind, the total pressure is perpendicular to the surface, and by the elementary laws of mechanics we can resolve this force into two components, *viz.*, an upward force, called the *lift* (which *lifts* or supports the weight of the plane), and a horizontal force called the *drift* (which represents the force with which the plane must be *driven*). By decreasing the angle of inclination of the plane to the horizon, we decrease the drift, but if the plane is *perfectly* horizontal, the wind will exert no pressure on it, so there will be no lift or drift at all. If, however, instead of using a plane surface, a concave curved surface of the same area is experimented with, it is found that greater lift and less drift are obtained, so that it is possible to support the same weight with less expenditure of power than before. This result holds good provided that the curved surface is inclined at a moderately small angle to the horizon. When its inclination to the horizon is considerable, the reverse is the case; there is greater drift and less lift than with the plane surface. But this is exactly what is wanted; for in order to stop a flying



machine it is necessary to tilt the aeroplane more nearly vertical, after the manner of a bird coming to rest. We want to check the horizontal speed as much as possible, accordingly the drift must be as great as possible, and here the concave surface is again the best.

Although most practicable designs for flying machines involve the use of the screw as a means of propulsion, Mr. Hargrave has constructed models working with flapping wings and finds little difference between the efficiency of this means of propulsion and a screw. But even here fixed aeroplanes were used in addition, and there can be little doubt that the ultimate form of the flying machine will be one supported on fixed planes driven through the air at high speeds. Several fanciful schemes for constructing gigantic air ships propelled by other means have been put on paper and have even lately appeared in print, but these must be viewed with suspicion. It remains to add<sup>1</sup> that Professor Langley and Mr. Maxim with small slanting planes have been able to support about 250 pounds per horse-power, exerted, and the latter, by using heavier weights, about 133 pounds per horse-power. Both of these figures, taken in conjunction with previous results, show that, so far as purely mechanical difficulties are concerned, the problem of flight is soluble.

(iii.) *Balance and stability*.—If it is of fundamental importance that a ship should be properly balanced and should not be liable to overturn, the same applies with even greater force to an aerial machine ; but the conditions to be satisfied in the latter are more difficult of investigation, and failure in this respect is attended with greater and more certain disasters in mid-air than on water. In his lecture to the British Association at Liverpool last year, Dr. Elgar pointed out that the stability of ships was not investigated mathematically till after many vessels had sunk, and that our present knowledge was only acquired as the result of considerable sacrifice of human life. The sad ending which befel Herr Lilienthal just when his experiments were beginning to be attended with their greatest success is the most unfortunate

<sup>1</sup> *British Association Nottingham Report*, p. 872.

one of a series of catastrophes which make it probable that we may pay as dearly for conquering the air as we have done in the past for ruling the waves.

Probably no experiments have contributed so largely to our knowledge of the conditions of balance and stability of aerial machines as those initiated by Lilienthal, and which have been brought to this sad termination. His work fortunately survives, and among his disciples there is no keener aeronaut than Mr. Percy S. Pilcher. On the other side of the Atlantic much valuable work has been done in the same direction by Mr. Octave Chanute, a former President of the American Society of Civil Engineers.

Remembering that the symmetrical form of all aerial machines experimented on is sufficient to secure what might be called their "transverse balance," the necessary conditions are really threefold, viz., transverse stability, longitudinal balance and longitudinal stability. It will, however, be convenient to deal with the two last together.

*Transverse stability*, or stability for rolling motions, is the only kind of stability which seriously affects the naval architect, who knows that it can be secured, so far as small displacements are concerned, by making a certain point called the metacentre—whose position he can calculate mathematically—above the centre of gravity of the ship. In an aerial machine various factors affect the corresponding kind of stability.

According to our ordinary statical notions the stability of any body in equilibrium can be increased by lowering its centre of gravity. It might thus appear at first sight that a soaring machine would be made more stable by bending the wings upwards at the tips, by raising the aeroplane, or by suspending a heavy weight considerably below the machine. But every shipbuilder knows that if a vessel is to sail steadily its centre of gravity must not be too far below its metacentre, otherwise the ship will roll from side to side in a heavy sea to a very inconvenient and even dangerous extent. So our ships are built with only a very small metacentric height; so small indeed that if the centres of gravity were raised a foot or so higher than their actual



positions the ships would become top heavy and overturn sideways. It remained for Pilcher to prove that a similar condition is equally essential in the case of aerial machines.

Pilcher's first machine had the wings very much upturned, and was provided with only a vertical rudder, not a horizontal one. But it was found that the machine pitched too much, so that it became rather dangerous to experiment on, and Pilcher then added a horizontal rudder which made the balance much better. He found, however, that although the **V** shape of the wings made the machine very steady when sailing against a head wind, a side wind was apt to tip it over, so he had another machine made with the tips of the wings flat instead of being curved up, but the wings were now placed at nearly the height of his head. Here again it was very difficult to balance with the weight so far below the wing surface, accordingly Pilcher took his first machine and bent the wings quite flat at the tips. He now found that by having the wings so much lower down he could balance much more easily; of course, if the weight were *too* high up, the equilibrium would be unstable; but Pilcher's experiments show that for safety the statical measure of stability must be small. On the modified machine form, Pilcher could sustain himself in the air for several seconds, and he was sometimes picked up by the wind and lifted as much as twenty feet above the ground; sometimes, also, he got some one to pull him along by means of a string, like a kite, or to hold him against the wind, and quite a moderate force was sufficient to hold the machine in mid-air. One of his achievements last Easter was to descend eighty yards in a calm, and noticing a large bush in the way he actually made the machine rise up in the air so as just to clear the obstacle. And on 19th June, he glided for over 250 yards in the presence of a number of spectators, an experiment which will be described in *Nature*, probably before the present article is in print.

Pilcher is hoping to get a small petroleum motor attached in order to make the machine self-propelling and thus convert a mere glider into a true flying machine. For an

eleven stone man, he says that no soaring machine should weigh more than sixty pounds, because it fags one out too soon, and the strain brought on is too severe. Many people seem to think that a machine can be fully tried in a few hours ; as a matter of fact it is only after having handled the apparatus for several long days for hours at a time that one begins to understand it at all.

The arrangement of two superposed planes used by Lilienthal in his latest experiments has not been adopted by Pilcher, although he took several sails from the top of Lilienthal's hill on the machine shortly before the death of its inventor ; the chief objection raised by Pilcher to the double surface being its unsteadiness in windy weather caused by the height of the upper surface—in short, its too great statical stability.

*Longitudinal balance and stability.*—Although it is essential for a ship to be properly balanced, the shifting of its centre of gravity slightly fore or aft would only cause the vessel to sink at the bows or stern and, even if the effect were considerable, it could easily be corrected before it led to any disastrous consequences. In an aerial machine, this longitudinal balance is much more difficult to deal with, since shifting the centre of gravity forwards causes the machine to dive downwards, and shifting it backwards causes the planes to tilt upwards and the apparatus to lose headway, become uncontrollable, and perhaps fall over backwards.

These facts, besides many others, can be verified by any one with the use of one or two gliders made of paper. It is only necessary to fold a sheet of paper down the middle so as to make it slightly V shaped and to load it with a small piece of stick to see how difficult this balancing is. Setting aside the fact that gliders have an obstinate habit of turning on one side instead of flying straight, the experimenter will probably lose patience before the glider can be balanced so that it will sail down steadily at an acute angle with the horizon.

But even after the glider has been properly balanced a certain amount of skill is necessary in projecting it at the



proper angle and with the proper speed in order to make it fly well, and, let it be remembered, every failure would represent a fatal accident on a flying machine. Instead of sailing uniformly, the glider will, as a rule, if fairly well thrown, describe a series of undulations in which, as in waves on water, the crests are narrower than the troughs : in short, curves much resembling a trochoid. To a mathematician it is a trifling transition from these crests to cusps, and from cusps to loops, and both of these forms are represented in the paths described by gliders, but the glider very often comes to rest and then falls down backwards instead of turning over and over. The general form of all the curves can be easily explained by the variations of the pressure with the relative velocity of the wind, and of the position of the centre of pressure with the inclination ; and I would suggest that a series of instantaneous photographs of the path of a glider, from which the forces and couples acting on it might be calculated, would afford an interesting means of verifying the laws of aerial resistance, just as the path of a planet affords proof of the law of gravitation.

The question next arises : Do the undulations remain constant in shape as the glider descends, or do the crests become more pointed till they become loops, or does the reverse take place ? If the second happens, the glider is longitudinally unstable and dangerous, while if the third happens it is longitudinally stable and safe. If the first happened the motion under proper initial circumstances would be stable but periodic, and any puff of wind might alter its character and cause the glider to upset, and moreover, if started from rest (*i.e.*, without initial velocity) the glider would certainly upset when it again came to rest. It is easy to build up an explanation of Lilienthal's fatal accident from some such considerations as these ; seeing that it is known that he actually was brought to rest by the wind, and in trying to get way on by tilting the machine forward, he fell right over and was killed. It is quite possible that had Lilienthal's machine carried a motor capable of restarting its forward motion at the critical moment, he might have been saved.

I know of no other mechanism in which this difficulty of longitudinal stability occurs except the old fashioned "Otto bicycle" where the rider sat between two large wheels, and the analogy suggests that the manipulation of a gliding machine is probably about as difficult to learn as riding *on one wheel*. This problem of longitudinal stability of aeroplanes does not appear to have been worked out mathematically. Experience has shown that a single surface of considerable fore and aft length is very unstable, and the narrow planes which are best for lifting are much better, but it is essential for stability that either a horizontal rudder or tail should be attached, or two or more planes should be placed one behind the other.

It is clear that if a change of inclination shifted the centre of pressure of a plane two feet wide through a distance of two inches, the shift for two separate planes each one foot wide would be only one inch, and consequently the combination would sail much more steadily, a result which any one can verify by experimenting with gliders. As regards the tail, the steadying action of birds' tails is sufficiently known, but it may be worth while to call attention to the fact that one of the most skilful of European butterflies in gliding flight, is the long-tailed swallow-tail (*Papilio podalirius*). The practical necessity of a tail in experiments on artificial flight was discovered by Lilienthal.

While birds are able to control their longitudinal balance by slightly turning their wings Lilienthal and Pilcher, experimenting with fixed wings, have been obliged to move their weight about in the machine, for which purpose they have supported themselves by their elbows only, leaving their legs free for the violent exertion required in tussling with a gusty wind.

Mr. Octave Chanute's experiments have, we believe, been directed towards obtaining a large machine that will glide steadily by itself without the performance of these gymnastic feats, and he considers that until this can be done, but little good can result from experimenting with motors. A number of successful glides have been made by him, many of them of considerable length. The successes



achieved by Professor Langley, which have been chronicled by the press, have consisted chiefly in the construction of a machine, driven by a motor, which has kept its balance continuously for a long flight. His model is not large enough to carry a man, and in the figures which appeared in the American papers, the addition of a person standing in the bows must be regarded as artistic licence.

(iv.) *Steering arrangements* need but little notice here. Lilienthal and Pilcher and other experimenters on gliding flight have acquired considerable skill in guiding their machines by balancing alone, and it is noteworthy that Lilienthal's fatal experiment was his first attempt at using a movable rudder. If aerial machines should ever be constructed on a large scale balancing will, of course, be out of the question, and horizontal and vertical rudders of some kind will be necessary, and it may be advisable that they should be experimented with soon.

(v.) *Strength and rigidity*, unlike the last conditions, are qualities with which all engineers are familiar. In the case of a flying machine this factor introduces peculiar difficulties as Maxim was not slow to discover. In order to keep a flat surface of considerable extent rigid, numerous struts and stays are required, and these Maxim finds add enormously to the resistance of the air at such speeds as are required for flight. Curved surfaces, as every mathematician knows, are better in this respect than plane ones. The only way of overcoming the difficulty seems to be to make the machine as small and compact as possible, and here the advantage of superposed planes becomes evident. Thus the conditions of rigidity are in no way antagonistic to the other conditions before enumerated. It is evident on the other hand that want of rigidity, by allowing the aeroplanes to bend, might considerably modify the stability of the machine.

In this connection I would call attention to the recent progress in kite flying since the subject was first taken up scientifically by Captain Baden-Powell in this country, Professor Hargrave in New South Wales, and others, which has resulted in the discovery that a box with open ends forms a most efficient kite, possessing far greater rigidity

than the old quadrilateral of our playgrounds, and, further, that the combination of two such boxes connected by horizontal bars, flies as a kite remarkably steadily and stably. Such matters as strength and *rigidity* can well be investigated by experiments with kites, which can be conducted at small cost and with little risk, while other more difficult investigations are being pursued by the students of flight proper. Moreover the old taunt of the French *plus léger* aeronauts that the *plus lourd* had never succeeded in ascending in the air has been completely met by Captain Baden-Powell's experiments in which people have ascended to considerable heights and descended in safety by means of kites.

(vi.) *Safe landing* has also been successfully accomplished by Lilienthal, Pilcher and others. It is most difficult to learn to land with a horizontal speed on. When beginning, one is certain constantly to tumble over forwards; the only way to stop is to get back in the machine and tilt it up in front so as to check the forward movement, thereby imitating the action of birds as revealed by M. Marey's photographs, described in his *Vol des Oiseaux*. Of course this is very difficult at first.

In order that this feat of landing safely may be accomplished, the machine must possess an aeroplane of large extent, such as will act as a parachute and encounter the greatest possible resistance. Another feature is that the machine must not be too large a one to be controlled by balancing. The stopping of a machine propelled by a screw presents difficulties. If the screw were reversed, the machine would simply be driven down on the ground. If the screw were driven forwards, it would have its horizontal motion increased instead of retarded. Pilcher proposes in such cases to stop the action of the propeller altogether, and rely on the aeroplane to stop him. The designers of large air ships are, as a rule, reticent on the means to be adopted for bringing them to earth.

*Summary.*—Now it will be observed that the conditions for a good flying machine, like the conditions of sensitiveness and stability of the common balance of our text-books, are to a certain extent incompatible. Every one of these conditions has been fairly satisfactorily dealt with by some



experimenters ; it only remains to embody them all in a single machine.

In what direction is the solution of the problem to be sought? If any experimenter can so thoroughly master the control of a machine sailing down-hill under gravity as to increase the size of the machine and make it large enough to carry a light motor, and if, further, this motor can be made of sufficient horse-power, combined with lightness, to convert a downward into a horizontal or upward motion, the problem of flight will be solved. The first flights need not be long—a hundred yards, rising, say, twenty or thirty feet above the ground, will be sufficient ; all else will be simply a matter of improving on the original model, and once success is assured workers will not be wanting.

Another promising direction for success lies in an elaborate and exhaustive investigation of balance and stability, such as would allow of the safe use of motor-driven machines too large to be controlled by mere athletic agility. This might partially be acquired by experiments with models, gradually increasing in size till they were capable of carrying a man and motor. But if the future development of artificial flight is not to continue a repetition of the chapter of accidents by which naval architects gained their theoretical knowledge, there is abundant work for mathematicians in reducing the conditions of stability of aerial machines to a matter of pure calculation. One thing is certain, till this is done designs of large air-ships for the wholesale transport of passengers, officers and cargo are not of the slightest value ; their designers would do better to study mathematics and help in the heavy work of calculation still requiring to be done.

Very different from the *air-ship* is the *flying-machine* by which it is sought to commence with small feats and gradually work up to big ones, and considering the number of workers at present in the field, and the scientific and systematic way in which they are studying the difficulties of their problem, we may yet hope that the realisation of artificial flight will take its rank among the scientific triumphs of the Victorian Reign.

G. H. BRYAN.

## ON PROGRESS IN THE STUDY OF VARIATION.

THAT variation is a subject worthy of study for its own sake is becoming recognised, and the numbers of naturalists who are devoting themselves to this study steadily increases. Probably, however, if the nature of the observations required were more generally understood progress would be much more rapid.

The first object of the study is to throw light on the origin of species. An exact knowledge of the facts of variation concerns many departments of biology, but it is in their bearing on the origin and nature of specific distinctness that these facts have their most direct and most manifest importance. It is, then, essential that the subjects chosen for investigation should be such as may be supposed to have this bearing.

Elsewhere (2) I have argued that it is reasonable to suppose that variations of a discontinuous nature may play a preponderating part in the constitution of new species, inasmuch as individuals presenting discontinuous variation in any character differ already from the normal of their own species—in respect of that character—much as one species differs from another.

For various reasons many have taken exception to this suggestion, and though I do not now propose to enter with any detail into matters of theory, nevertheless it may be well to note the fallacy of one line of reasoning upon which objectors have especially relied. It is said for example that discontinuous variation is an exceptional phenomenon, that “sports” are so rare that they may be neglected, and that the appearance of discontinuous variation often seen in collected series of specimens is due to an arbitrary system of collection. These objections are founded partly on an imperfect understanding of the suggestion that discontinuous variation may be a chief factor in evolution, but far more often they proceed from a want of familiarity with the class of facts upon which the suggestion is based.



First, it is evident that there is considerable misapprehension as to the sense in which the term discontinuity is used in its application to variation. Discontinuous variation is carelessly supposed by some to be synonymous with "sport". While however a sport is a discontinuous variation, it is not in this restricted sense that the term should be used. The word "sport" is generally used to denote a variation connected with the normal by no intermediate individuals. In many—perhaps in most—cases of discontinuous variation there is a complete series of intergrading individuals, not necessarily in each direct line of descent, but occurring among the varying population. Discontinuity in variation is a term of degree. A variation is discontinuous *in proportion as* intermediates between the variety and the type are comparatively infrequent. For a variation is discontinuous if, when all the individuals of the population are breeding freely together, there is not simple regression to one mean form, but a sensible preponderance of the variety over the intermediates. When such a population is seriated in respect of the varying character for statistical study in the manner with which naturalists have been familiarised by the writings of Galton and others the curve of variation has not one peak as in a monomorphic species, but has at least two peaks. The essential feature of a discontinuous variation is therefore that, be the cause what it may, there is not complete blending between variety and type. The variety persists and is not "swamped by intercrossing".

While the word "sport" is expressly used to denote something rare or monstrous, no such idea necessarily attaches to discontinuous variation. When in a species commonly known to us as a constant and comparatively invariable form, an individual is found showing a striking variation, we call it a sport. Thus the six-rayed *Sarsia* ((2), p. 424) is a sport. But in some Medusæ the presence of individuals exhibiting similar meristic variations, either regular or irregular, is so frequent that these "sports" are a normal constituent in any sample.<sup>1</sup> If in England a speci-

<sup>1</sup> For example *Aurelia*, see Browne, Q. J. M. S., xxviii., p. 245; various authors *Nature*, 1894; *Zool. Cblt.*, ii. p. 37, etc., and *Eucope*, Agassiz and Woodworth, *Harv. Bull.*, Nov., 1896, p. 121.

men of *Argynnis adippe* were captured having the silver spots on the underside of the hind wing absent we should call it an extraordinary sport; but in most subalpine localities such specimens are common both in *A. adippe* and *A. niobe*. In the latter species in fact it is the silver-spotted form which is exceptional in many localities.

In any extended view of variation it is soon apparent that a variety which in one species and one locality is exceptional, may in another species or another locality be of constant occurrence.

So also in regard to the reiterated assertion that the appearance of discontinuity between type and variety is due to the arbitrary rejection of intermediate forms. It is true enough that in very few cases are proper statistics forthcoming, and that as yet it is impossible to say *how much* discontinuity exists in any but a few examples. Nevertheless the fact that in innumerable cases the type is common, and a variety is common relatively to the intermediate forms is familiarly known to collectors. Everything depends on the species and the variety chosen for illustration. For example, in the moth *Callimorpha hera* the hind wings are generally red, but a yellow variety is common. In this species it happens that specimens of intermediate tints shading through orange and buff are frequent. So far as I know it has not been established statistically that the intermediates are less common than the yellow variety, and possibly enough they are more common. But in *Thais medesicaste* the discontinuity between the type and the variety *honoratii* found flying with it at Digne, in which the yellow of several cells wings is replaced by red, cannot be questioned. The intermediate forms are either absent or quite exceptional, though type and variety occur together.<sup>1</sup>

The further we proceed in the study of variation the clearer it becomes that we have no warrant for applying the conclusions as to variation and inheritance derived from the

<sup>1</sup> In illustration of the want of blending in this case it may be mentioned that a specimen was reared by Standfuss ((8), p. 319) which was *honoratii* on the right side and *medesicaste* on the left.



examination of one species or one character to the problems presented by other species or other characters. The properties of species are in brief *specific*, as the properties of chemical substances are; and as the properties of each chemical substance have to be separately determined, so must the specific properties of each species be the subject of separate and special study. In what may be called the Chemistry of Species we are far indeed from the era of generalisation.

Discontinuity in variation is in great numbers of cases an observed fact, while the supposition that when organisms are freely breeding together in the state of nature all the varieties they display in size, colour, structure, and so forth, are capable of freely blending, and that the offspring of dissimilar parents tend always to regress to one mean form is not borne out by the facts. Whether continuity or discontinuity is found depends on the species studied and the character selected for investigation. There is continuous variation, but there is discontinuous variation also. To discover by statistical investigation the degree of continuity or discontinuity which in each species is manifested by the variation of each character is the first business of the student of evolution.

Those who do not admit the probability that discontinuous variation may have a preponderating influence in the establishment of new species will remember that this is confessedly a matter for individual judgment, and whatever views may be entertained on this matter the fact that discontinuity is frequent in variation remains indisputable. Indeed, if it is admitted that the problem of evolution is to be attacked by the study of variation no assumption need be made to justify the prerogative claims of cases in which there is an appearance of discontinuity; for discontinuous varieties have, *prima facie*, already something of specific distinctness, and whether they are or are not those nascent species we are all seeking, they at least look more like them than other varieties do.

We are in a preliminary stage, and apart even from any question of continuity or discontinuity it is surely well that

those who are contemplating systematic investigation of the problem of species should begin by the study of such cases as these. It is, in short, reasonable that the study of variation should be begun with the systematic study of varieties.

By disregard of this limitation a greater scope for statistical refinement may be rendered possible—for the observer is thus free to choose the subject most amenable to such treatment—but it may be questioned whether the compensation is adequate, and whether the solution of the particular problem of the nature and origin of specific differences is greatly promoted thereby.

With this limitation, however, begins a real difficulty, one that it must be feared will for long beset the serious study of evolution. In order even to choose subjects for his inquiry, still more in order to pursue them, the student of evolution needs the peculiar knowledge and experience—the whole apparatus, in fact,—which only the collector possesses. In all this he is too often deficient. It is much if the very names of common objects of natural history are familiar to him, and the world of “good species” and “bad species” is unknown. Seldom even can the two classes of men greatly help each other. The collector finds the evolutionist ignorant of what he regards as the rudiments; he only vaguely perceives the other’s purposes and is not greatly interested in them. His collection was made with different objects altogether, and though with the best will in the world he puts it at the service of any one who will work at it, he cannot make it serve a purpose for which it was not designed. The other leaves disappointed. His questions are mostly unanswered, and he is tempted to feel that the methods of the collector are narrow and that he has missed his opportunities. Now both men are right. The future is with the evolutionist, but it is the collector who has made it possible for him to begin his work.

The time has surely come for some attempt at closer collaboration between these two classes of students. Collecting in the ordinary sense, amassing once more the specimens of each species and variety in thoroughly familiar ground, such as England and Central Europe, is a well-



worn pursuit from which little novelty can be hoped. Such collecting is little better than a pastime, a thing of momentary value. On the other hand, by only a slight modification in his practice the collector could make his collection a body of evidence of high scientific value, evidence which if we are to progress with the problem of species has become a necessity. Not the less will he find in his work the peculiar fascination which collecting exercises over so many minds.

What the evolutionist asks of the collector is simple. It is, in brief, that he will give to the collection and observation of a few—and for choice, variable—species, the time and effort that he now devotes to the bringing together of rarities. This is a very simple thing, but I believe that at this moment it is a work which scarcely any one has in hand. Scattered over the world there are hundreds of people employing their energies and exercising a high degree of skill in the collection of natural objects and in breeding specimens for their cabinets. If only a few of these had set to work in the way required, we should perhaps already know a good deal about the origin of species.

The fancy is common that in order to investigate evolution, experiments of an elaborate character, dealing with the causes of variation and other recondite subjects, are essential. This is a complete mistake. The first requirement is to know the plain facts as to the occurrence of species and their varieties in the state of nature. To pursue the question of the interrelations of these forms and the degree to which characters are inherited, artificial breeding must of course be undertaken; but even such breeding involves in some cases little more than what many of the best collectors—Lepidopterists at all events—are already undertaking for the sake of rearing perfect specimens.

It may be remarked that variation is conspicuously a subject which can be studied by simple means. Since, moreover, it is essential that each observation should be made repeatedly by different observers in different localities, for a long time no one need fear that he is uselessly

traversing exhausted ground. We are still at the very beginning.

In what follows I purpose to take a few examples, most of them easily accessible, in illustration of the work in view, hoping that those who propose to devote themselves to such questions may be thereby assisted in the choice of a subject, and that these illustrations may afford some indication of the methods which are required. While specialists will already be familiar with most of the subjects chosen, to students of evolution there will be nothing novel in the statement of method.

Variations so definite as to suggest that they may possess something of specific distinctness may roughly be divided into two classes. In the one the variety is found associated with the type, mingling and, we must suppose, breeding freely with it; in the other the variety is found partly or entirely separate from the type. It is perhaps especially in dealing with cases belonging to the second category that we stand in the greatest need of the co-operation of the general collector; but in order to explain more clearly the particular treatment which is needed in cases of the second class, two examples of the first and simpler kind may be conveniently spoken of.

The first is an example of variation familiar to all entomologists, that of *Amphidasys betularia* L. and its variety *doubledayaria*, Millière. The typical form is the well-known Peppered Moth, a large insect having the whole upper surface of the wings of a white ground colour, almost uniformly speckled with black. The sexes are similar. Of this insect a unicolorous *black* form, the variety *doubledayaria*, is now commonly distributed over the northern and midland areas of England. The special interest of this case lies in the fact that it is one of the few examples in which a variety is known to have come into prominence within recent times. Though the case is notorious in entomological circles its importance has scarcely been recognised by evolutionists. A short summary of the evidence is given by Barrett (1), see also Chappell (3). Briefly the



facts are that this striking black variety, of which the early entomologists say nothing, was first met with as a rarity in the North of England towards the end of the forties. It was figured and named by Millièrè (6) from an English specimen. The variety lives on the various food plants of the type. In 1865 it is reported that most of the males attracted by females exposed at Manchester were of this dark form. In a few years it had spread through a great part of the Midlands. In 1870 the black form was almost as frequent as the type at Newport, Monmouthshire, and a few years later the typical form had almost entirely vanished from that district. At Chester none but black specimens have been met with for many years. In recent years casual specimens have been taken in various English localities as far south as Berkshire. On the continent the appearance of the black variety was much more recent. A dark specimen—though not so dark as *doubledayaria*—was recorded in Belgium in 1886 (4), and again intermediates are reported from Belgium in 1894 (5). In the past ten years the black form has spread over a great part of Germany, as far as Silesia and Dresden (8) (p. 316).

Here then is an actual case of the establishment of a natural variety. If only the Lancashire entomologists had put by 100, or even twenty, specimens of *betularia* taken at random year by year, what a splendid record it might have been! But though there is no such complete evidence as this, the leading fact is clear. In a short time, some fifty years, a dark form has supervened on the light one. Now did this come about by the gradual shifting of the average form through all stages of grey to black? It is practically certain that it did not. The change came about by the success of a particular dark strain or strains. Not that it must be supposed that intermediates are unknown. On the contrary, Mr Barrett, who kindly showed me several of them, tells me that he believes that they were formerly more common than they are now. Moreover, in Belgium it seems clear that an intermediate strain has established itself, and intermediates are also said to be plentiful in the Rhenish Provinces and Westphalia, together

with totally black forms. In some parts of this district, however, as in Barmen and Crefeld, the typical *double-dayaria* is said to be already the commonest form (8). But there is no doubt both that the totally black form existed at an early stage in the transformation side by side with the light one, and that in localities where both occur the same is still the case. The course has not been that the insects of each successive district have become more and more tinged with black, till they culminated in *doubledayaria*, but rather that *doubledayaria*, or less often one of the intermediate forms, spread into, or at least appeared in the area, and either co-exists with the type or has replaced it.

There is great need for experimental and quantitative evidence as to the inheritance in crossed and thoroughbred strains, and the subject is probably well suited to such work. Nevertheless the results of the few experiments that have been made are in accordance with the expectation based on the simultaneous occurrence of the forms in nature, that there is imperfect blending between type and variety, for Steinert (9) raised from a typical black wild female found at Dresden a brood consisting of seventy-five *betularia* and ninety *doubledayaria*. Two of the *betularia* were slightly darker than the normal form.

Similar changes are said to be taking place in several other British species of Geometræ, but the evidence seems to be less clear and less extensive than it is in the case of *betularia*.

Here, then, we have the means not merely of studying the relations of variety to type, but also of actually witnessing a case of evolutive change. If some one will make it his business to collect samples of *betularia* from various districts he will certainly make a valuable contribution to the science of evolution. All that is needed is that wild samples should be taken at random, fairly illustrative of the population of each district, and sorted into classes, (1) normal *betularia*, (2) light intermediates, (3) intermediates, (4) dark intermediates, (5) typical *doubledayaria*. A simple way by which something might be done would be to arrange year by year for the exposure of a few fresh females reared in



captivity, when the attracted males could be taken in the way often followed with such species. This would of course only give information as to the male population, but that would go far towards answering the question.

The numbers which it would be desirable to collect in each sample should of course be as large as possible, but there is a tendency among those not practically acquainted with such problems to greatly exaggerate the need for excessive numbers. To rightly assess the importance of minute and insensible variations, doubtless vast numbers of individuals are needed, but in cases like that of *betularia* probably a very moderate number would in the first instance suffice to give a broad but reliable indication of the facts. If in 100 specimens<sup>1</sup> there were thirty dark and ten intermediate, the subsequent collection of 1000 would probably change the absolute percentages a little, but it is unlikely that it would materially modify any conclusion based on the first sample.

No doubt in districts where the variety was very scarce large numbers would be needed, and it is doubtful whether such cases are suitable for statistical investigation. In the Cambridge district, for instance, *doubledayaria* is still almost unknown. In addition to a typical specimen of the variety I lately took, I can learn of only two others, which were taken severally some years ago. The ordinary form, however, is common, and it is likely that a few hundred specimens would contain no *doubledayaria* at all.

In order to follow up the statistical study of wild specimens and to obtain experimental proof of the modes of transmission of the varying characters by artificial breeding, a wider range of observation is necessary, and, from a few experiments only, contradictory results are almost sure to follow.

The difficulty arises especially from the fact that the power of transmission of the individual is undoubtedly affected by its own back-breeding, a quantity for the most part unknown. In illustration of this I may refer to the discrepancy between the results obtained by Burckhardt,

<sup>1</sup> It is assumed, of course, that the specimens are collected in such a way as to preclude the possibility that they are all one family.

referred to by Standfuss ((8), p. 307), in crossing the varieties of *Spilosoma lubricipeda* and the results obtained by several observers in this country working with the same species. It is well known to entomologists that of this species there is a peculiar dark form, *zatima*. Cram. found in Heligoland.<sup>1</sup>

This variety has been observed to breed true when paired (7). Now there is good evidence that when the Heligoland variety is crossed with the type, the offspring may consist of the type, of true *zatima*, and of certain lighter forms of this variety, named var. *intermedia* of Bang-Haas. But between this latter variety and the type, though crosses of the most various nature were continued for four years and an immense series of specimens reared, the intermediates were always wanting (8). But this is not because such intermediates cannot exist. In England a dark race of *lubricipeda* has been artificially reared by selection (starting from naturally dark specimens) by the Yorkshire entomologists, which approaches rather nearly to the true *zatima*. These artificially produced forms are known as *radiata*. In a series of them belonging to Mr. Porritt's strain, kindly shown me by Mr. Barrett, are many of both sexes which quite fill up the gap between *intermedia* and true *lubricipeda*. Still more completely is this interval filled by a series lent me by Mr. W. H. B. Fletcher, which had been reared by crossing the partially artificial *radiata* with another variety.

Again Standfuss records that by crossing the natural dark variety *eremita*, a form of *Psilura monacha*, with the type, a brood was produced containing one female *eremita*, the rest being all typical *monacha*. This cross-bred female he again crossed with a male of the type and there resulted twenty-two normal *monacha*, twenty-three typical *eremita*, and six individuals in which the characters of type and variety were *asymmetrically* mixed. Such a brood is a clear proof of imperfect blending of the two characters.

<sup>1</sup> Whether it is there associated with the type or not I cannot find clearly stated by any authority, but I gather that the normal as well as the variety occurs in the island.



But Mr. Fletcher by starting with a normal female *monacha* raised by selection among her offspring, successively repeated for five years, a series of which a few in the latter years are practically *monacha*, and in this series numerous intermediates occur.

In each case the indication is the same, that the results depend on the strain employed. It is greatly to be hoped that these experiments may be repeated and detailed statistics of the results published.

So far as I can learn those that have been hitherto performed have not been for the most part recorded in any detail and the specimens have been largely dispersed.

The other case which I shall take in illustration of a similar phenomenon is that of the hairy and smooth forms of the Cruciferous plant, *Biscutella lævigata*. I have had opportunities of observing this plant in several localities in the wild state, and in a recent communication to the Royal Society Miss E. R. Saunders has given the results of experimental cultivation and artificial fertilisation of its varieties. The facts are these. The plant is a common Alpine species with a rather wide distribution. Some authorities describe it as hairy, others as glabrous. Generally it is stated that it may be either hairy or glabrous. The essential fact to the student of variation is that in certain localities the hairy and the glabrous forms may occur side by side in the same meadow or on the same rock. In my experience the hairy form is the commoner. The plant is common, for instance, in the Val d'Anniviers, at Bérissal, near Airolo, and elsewhere, exclusively in the hairy form. The leaves and stems are thickly covered with a short pubescence, varying in texture, but commonly the hairs are stiff. But in the Val Formazza, side by side with the hairy plants, are others exactly resembling them in the rest of their structure, but having the surfaces of the leaves and stems smooth and devoid of hairs. In the great majority of these smooth-leaved plants, however, the margins of the leaves and the leaf-teeth, often also the mid-rib, bear hairs: it is the *surfaces* which are smooth. In this valley, both

above and below the Tosa Falls, the plant abounds in both these two forms, the smooth being on the whole the more abundant. Now between these two there are various intermediate forms making a complete series connecting them. But though the degree of hairiness varies, and the degree of smoothness varies, the immense majority of plants in the locality can be referred unhesitatingly either to the hairy class or to the smooth. Plants which are so intermediate in character as to cause the observer any doubt as to the class to which they belong are decidedly scarce. Owing to the fact that the plants increase much by runners, forming new crowns which afterwards separate, it is impossible to say which should be counted as "individuals," and hence it is not easy to see how a reliable numerical measure of the discontinuity can be obtained, but that the fact is substantially as stated there is no doubt.

The question then arises, how is it that these two distinct varieties can exist side by side, exposed to the visits of insects, without regressing to the mean form, which, as was stated, is comparatively scarce? To determine this Miss Saunders made artificial crossings of the two varieties in the Cambridge Botanic Gardens. The mongrel seedlings, judged by their first few leaves, consisted of some hairy, some smooth, and a large number of various intermediate forms. But it was found that as these seedlings grew older, while the hairy continued to put up leaves which were hairy, the intermediates in their later leaves turned to smooths. The original smooths also to some extent became smoother. When, therefore, the well-grown mongrel plants are examined they present just the same appearance of discontinuity which the wild plants at the Tosa Falls do. This discontinuity is, therefore, the outward sign of the fact that in heredity the two characters of smoothness and hairiness do not completely blend, and the offspring do not regress to one mean form, but to two distinct forms. The variety, in short, is not "swamped by intercrossing".

Which may be the older form we will not venture to discuss. It is, however, of no small interest to note that Miss Saunders found that the smooth plants suffered far



more from slugs—which attack the species greedily—than the hairy ones did. We have no information on the point, but it is just possible that some creature which elsewhere eats off all the smooth seedlings is absent from the Val Formazza. The eggs of *Pieris napi* are laid on both kinds, and the larvæ can eat both kinds, but whether they prefer either I cannot say.

These two cases must suffice as examples of those varieties which, coexisting with the type, have the quality of distinctness. Many such cases will be known to those who collect animals or plants. Of few indeed have any satisfactory accounts, much less statistical records, been prepared showing how or in what proportions the various forms occur in nature; and in still fewer has any cross-breeding been systematically carried out. In most cases all that we know is the bare fact that such a species has such a variety commonly or occasionally found associated with it, if so much. Rarely do we know for certain whether intermediate forms exist or not. On such points the writings of systematists are too often consulted in vain.

In all these cases the course to be followed in the first instance is simple, and consists in examining and, if possible, preserving a fairly numerous sample taken at random from as many distinct localities as possible. In recording the results of such collecting, the essential points to be noted are these:—

- (1) That the variety occurs associated with the type; that it is scarce or abundant.
- (2) Whether the variety is connected with the type by a series of intermediate forms or not.
- (3) If intermediates do occur, it is then to be determined whether in each sample the specimens can for the most part be readily sorted into type and variety, or whether specimens that are so intermediate as not to be thus referable are common.
- (4) The above questions to be answered separately for each sample from a distinct locality.

With regard to the third point, it is obvious that when-

ever it is possible the numerical proportions which the type, the variety, and the intermediates bear to each other should be determined carefully by statistical seriation. This must be done in suitable cases by measurement, and in other cases by the constitution of a series of grades and counting the specimens belonging to each grade. But even where by the intrinsic circumstances of the case or by the conditions under which the collecting or observations have to be conducted, numerical estimations cannot be made, it is certain that most valuable material would be provided merely by answers to the first two questions, with a careful statement of impression as to the third point. These answers would not merely show roughly whether the case was likely to repay further and special investigation, but they would provide that general outline of the properties of species in regard to variation which all the labours of the systematists have failed to provide, though it has become an urgent necessity to progress. The systematists have given us a catalogue of the material, treating it from the cataloguer's standpoint, but in the light of the study of variation we are still at the first recension.

In a subsequent part the application of these methods to the special problems presented by local races will be considered.

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(*To be continued.*)



## THE APPLICATIONS OF CRYSTALLOGRAPHY TO PHYSICAL CHEMISTRY.

THE chemistry and physics of gaseous substances have been for so many years the subject of such careful study that we are now in possession of complete and highly organised working hypotheses respecting most of the properties of gases. And although it can hardly be said that the facts up to the present elicited from the study of liquid substances have led to the establishment of satisfactory theories concerning the molecular physics of liquids, yet the pioneer work has been so well done that we are within measurable distance from the acquirement of very complete knowledge of the molecular constitutions and molecular tactics of liquids; the methods of attacking the problems involved, which have been based on such properties as the molecular volume, refractive power, capillarity, viscosity, thermal properties, etc., are of so powerful a nature that the situation will probably be to all intents and purposes captured within a very few decades.

Whilst, however, the great measure of success which has attended scientific inquiries into the molecular properties of liquids and gases must stand as an abiding monument to the industry of the nineteenth century, our comparative ignorance of the chemistry of the solid state will, in years to come, testify to that high order of unassailability peculiar to the questions at issue which seems to have almost nullified all attempts to learn something of this department of chemistry. That we know multitudes of facts respecting solids cannot be denied, but it is scarcely an exaggeration to say that the framework of chemical theory surrounding those facts is of too flimsy a nature to hold them together, and the absolute value of the theories as affording indications of the lines upon which future work should be conducted is extremely small. We learn little of scientific importance from most of the physical or chemical facts at present known about solids; such a fact as that the great tough-

ness of pure copper disappears in presence of a trace of alloy, although of much practical importance to copper-smiths and to engineers is scientifically barren, because it has not yet tended towards the attainment of the only aim of all scientific work, namely, the acquirement, at some infinitely distant date, of a perfect knowledge of the constitution of matter.

The history of the physico-chemical investigation of gases, liquids and solids is of the very highest interest, not only as teaching the classic methods which have done such service in the past, but also as indicating the lines upon which work will probably be conducted in the future. Comparatively early in the century the physical and chemical examination was prosecuted with an energy which rapidly furnished us with a fairly complete theoretical knowledge of gases; and it was not until much later that a vigorous attack, directed against the more complex problems presented by liquids and liquid solutions, led to a vast increase in our store of knowledge of matter. It cannot be doubted that in the future the investigation of the physico-chemical properties of solids will be undertaken by chemists with a unity of purpose which will speedily bring to comparative maturity our present embryonic knowledge respecting solids. Under these circumstances it may not be unprofitable to consider some few of the peculiarities which stamp solids as a class apart from liquids or gases, and to point out in what way these peculiarities affect the questions at issue and how they may easily lead astray.

Many of the laws governing gases are immediately applicable to liquids, the differences between the two states being largely differences of degree and not of kind; the truth of this statement has been repeatedly exemplified by the masterly work of van der Waals on the continuity of the liquid and gaseous states and by many other investigations published during recent years. The brilliance of the results which have been obtained by drawing analogies between liquids and gases would at first sight seem to stamp as logical those attempts to learn something of the physical chemistry of solids which have been based on analogy; but



as indicated above little absolute difference of kind exists between liquids and gases, and it is consequently advisable, before attempting to apply laws governing these two states to solid substances, to inquire whether the differences between solids and liquids are also, in the main, differences of degree rather than of kind, and, if considerable differences of kind do exist, to ascertain whether they are of a nature likely to vitiate arguments based on analogy.

At the very outset of the inquiry we are met by a well-marked difference of kind between solids and liquids. The particles composing a liquid are free to move, and under ordinary conditions bear no fixed and definite orientation one to the other; although Perkin's work on magnetic rotation probably indicates that under certain conditions, as when placed in a magnetic field, the particles of a liquid do arrange themselves in some regular manner. Almost all solid substances, however, are crystalline and an amorphous or non-crystalline solid is a substance of some rarity, most substances which are casually described as amorphous being in reality crystalline. That the arrangement of the particles of a crystalline body is not a structureless or amorphous one is evident from a very superficial examination of such properties of crystals as the colours, solubilities, electrical properties, cleavages and refractive indices; these properties being different in different directions in the crystal demonstrate conclusively that the arrangement of the parts or structural units of the crystal varies with the direction. And we are now, thanks to the labours of Sohncke, Barlow and others (compare Miers, *SCIENCE PROGRESS*, 1894, i., 483; 1896, iii., 129), acquainted with all the possible kinds of arrangement of these units of the crystalline structure. It is important to consider in what way this homogeneous arrangement existing in crystalline substances but not in liquids or gases can affect analogies drawn between liquids and gases on the one hand and crystalline bodies on the other; the best method of showing the kind of disturbance introduced and the ways by which it may be eliminated is probably to consider a few actual cases.

The careful study of the refractive indices of liquids and

gases has shown that a refraction constant of an additive nature—termed the molecular refraction—can be calculated; if  $W$  be the molecular weight of the compound,  $d$  its density and  $n$  its refractive index for a particular wave-length of light, the molecular refraction  $R$  is calculated from the equation :—

$$R = \frac{W}{d} (n - 1).$$

On determining the molecular refractions for a large number of organic liquids, Gladstone found them to be the sums of so-called atomic refractions of the atoms composing the molecule of weight  $W$ ; these atomic refractions are themselves calculated from the observed molecular refractions of many liquid organic compounds. It is found further that the atomic refraction of a carbon atom attached to four different atoms or groups of atoms is different from the atomic refraction of a carbon atom bound to only three atoms or groups of atoms; the same is true of other atoms bound to different numbers of other atomic groups. A knowledge of the molecular refraction is frequently of great value to the organic chemist, as for instance in determining whether any particular organic compound is saturated or not, namely, whether any of its carbon atoms are attached to less than four other atoms or groups of atoms, because the molecular refraction of a saturated compound differs from that of an unsaturated compound of the same molecular composition. On attempting to apply the idea of molecular refraction to crystalline substances, difficulties arise, because in the cases of most such bodies the refractive index varies with the direction; it is thus not at first sight clear how the varying refractive index of a crystalline substance can be dealt with so as to yield a single molecular refraction constant from which results analogous to those obtained in the case of liquids might be derived. It has, however, been shown that from the several refractive indices of a crystalline solid a certain mean refractive index can be easily calculated which would be the refractive index of the substance if the regular arrangement of its particles were destroyed whilst its density were maintained constant; then



by using this mean refractive index to calculate a molecular refraction by the formula quoted above, it is demonstrated by taking many examples that the molecular refractions of crystalline salts are, like those of organic liquids, additive quantities within the limits of experimental error, that is to say, the molecular refractions are the sums of the equivalent refractions of the atoms or groups of atoms (radicles) composing the molecules.

Evidently, in the foregoing case, the differentiated structure of crystalline substances prevents the immediate application to them of a law governing liquids and gases although the hindrance so introduced can be put aside by a comparatively simple operation. In the case of other properties of crystalline substances, however, so simple a method of eliminating the complication introduced by the structure will scarcely avail, although the method adopted above for maintaining the analogy by a process of averaging will doubtless be ultimately found applicable to a large number of properties.

Thus the famous law of Dulong and Petit which states that the product of the specific heat and atomic weight of an element is a constant, is only a very rough approximation to truth. This is doubtless due to the fact that the specific heat is not wholly dependent on the nature of the element but partially also upon the crystalline form of the element; we know that two different crystalline forms of the same chemical substance possess different specific heats as in the case of diamond and graphite or of crystalline and amorphous selenium. This quite apart from the apparent necessity of obtaining data, not at the same temperature but at equivalent temperatures, namely, at equal distances from the critical temperatures of the substances concerned, is a sufficient reason for the failure to so modify the law as to make it exact; since the specific heats are measured on elements the crystalline forms of which are totally dissimilar, the influence of the crystalline structure on the specific heat is wholly irregular and consequently no simple law could govern the data with rigid accuracy. Only after the specific heats of the elements have been calculated from the specific

heats of the liquid substances or their compounds under comparable or equivalent conditions apparently will it be possible to re-cast the original law into a form in which it will hold with accuracy. Naturally, the same kind of criticism is applicable to many other properties, such, for example, as the electrical conductivity; since all the solid metals and most other substances we have to deal with are crystalline, composed of minute crystals of which the conductivity varies with the direction and of which the average conductivity is presumably dependent on the crystalline form, no general quantitative law connecting the electrical conductivity and the chemical nature of the material can be formulated until the influence of the crystalline form of the tiny individual crystals can be expressed in figures and eliminated.

Many other instances might be quoted in which crystallographic causes operate to render obscure the laws governing various classes of chemical phenomena; an instructive case of the kind arises in connection with the heat of formation. During the formation of a chemical compound by the union of certain materials a perfectly definite quantity of heat—the so-called heat of formation—is absorbed or liberated; this heat of formation is of course a measure of the energy-content of the compound. The heats of formation of substances have long been regarded as a highly constitutive property, the continued study of which cannot fail to yield important information respecting the manner in which the atoms constituting a chemical molecule are linked together; large numbers of organic compounds,—gaseous, liquid and solid—have therefore been examined in order to ascertain the exact nature of the relation holding between chemical constitution and heat of formation. The results up to the present obtained have hardly been commensurate with the work done on the subject owing to the many inherent difficulties which have been encountered. It is, however, somewhat remarkable that the influence which the crystalline form of a solid exerts on its heat of formation has to a large extent escaped consideration so that we find, for instance, the heat of formation of solid substances compared with those of



other and liquid compounds ; further, the crystalline characters of the solids examined are scarcely ever specified. The kind of misunderstanding to which this may lead is well exemplified by the following case. The curious statement has been on record for many years that the latent heat of fusion of chloral hydrate prepared immediately before examination by melting and then solidifying is less than that of the same material solidified some days before examination ; this mysterious result has a purely crystallographic cause which completely escaped the notice of the original investigators. Crystallographic examination of chloral hydrate shows that when it solidifies from the molten state it crystallises in long thin needles ( $\beta$ ) but during the following ten days or so these needles slowly change into stout rhomboidal plates ( $\alpha$ ) until finally the whole material consists of plates formed at the expense of the original acicular form ; the explanation of the variable heat of fusion is now simple. The  $\beta$  modification of chloral hydrate has a low latent heat of fusion, only about one half that of the  $\alpha$  form ; during the prolonged and gradual conversion of the  $\beta$  into the  $\alpha$  modification the difference between the two heats of fusion is as gradually liberated and dissipated, the result being that to convert the  $\alpha$  modification into liquid at the same temperature requires the absorption of about twice the quantity of heat necessary to liquefy the  $\beta$  modification under similar conditions.

Examples such as the above, indicating the important influence of the crystalline form in complicating physico-chemical problems relating to solid bodies might be multiplied indefinitely but all point the same moral, namely, that since the crystalline form is practically always a complicating feature, it is an imperative necessity that all exact work on solids, whether chemical or physical, should be accompanied by a careful study of the crystallographic questions involved ; until the original investigator, more especially the physicist, recognises and acts upon this conclusion, his work on solids, though doubtless of much value in the workshop, will be comparatively unfruitful of results of scientific interest.

The intimate connection of crystallographic phenomena with many physico-chemical problems relating to solids having been thus pointed out it is of some interest now to consider what views respecting the chemical constitution of crystalline bodies are possible and reasonable, and how these may be expected to affect physical chemistry; the chemical constitutions of crystalline substances have long been a favourite theme for discussion, but owing to the very gradual accumulation of facts the last word on the subject will long remain unsaid.

A considerable proportion of crystalline substances exist in several forms which differ crystallographically amongst themselves and are consequently termed polymorphous modifications of the same compound; thus the  $\alpha$ - and  $\beta$ -forms of chloral hydrate are polymorphs. Since polymorphs are in general very readily converted one into the other by change of temperature, and their properties would seem to differ only in physical and not in chemical respects, it is generally considered that the chemical molecules in the various polymorphous modifications of a compound are identical; and inasmuch as the physical properties differ markedly it has, until recently at least, been customary to presume the existence, in polymorphous modifications, of physical molecules composed of aggregates of chemical molecules, the number of the latter constituting these aggregates being different in the various polymorphs. This distinction, being very vague and perhaps somewhat metaphysical in tendency, has like many of the household terms of physics and chemistry, proved invaluable as a disguise to our ignorance; although from its very nature somewhat difficult to attack, the notion of a distinction between physical and chemical molecules has a weak point in that it is at present quite unnecessary. Tutton, from a consideration of the results of much experimental work in the light of Barlow's investigations into crystalline structure, has demonstrated the probability that, at all events in the cases which he has examined, a crystal is built up merely of chemical molecules, and that these are not necessarily aggregated together in any such way as is



suggested by the idea of physical molecules; we may, however, take a step beyond this and point out that so far as our present knowledge goes there is little foundation for the view that amongst polymorphous substances the units of which the crystalline structure is built up are other than simple chemical molecule.

Barlow has shown that by distributing an infinite number of bodies in space in such a way that the arrangement around each is in all respects similar, a number of arrangements are obtained each of which has exactly the symmetry of one or other of the thirty-two crystalline systems; it is obvious that no direct relation exists *à priori* between the symmetry of the system of bodies and that of the component bodies or figures themselves. We must conclude from Barlow's work that a crystal is simply a system built up of particles which do not in general possess the same symmetry as the system itself, and which we may suppose to be the so-called physical molecules. Now in the case of a substance like calcium carbonate which exists in two polymorphous forms, namely as the hexagonal mineral calcite and the orthorhombic aragonite, it seems to demand fewer assumptions to suppose that the physical molecules are the same in the two minerals, the only differences lying in the nature of the mode of distribution of the molecules, than to assume that the units of which the crystalline structure is built up are of different complexity in the two cases. Many substances, like ammonium nitrate, exist in several forms, each of which is stable within certain limits of temperature but changes into another polymorphous modification so soon as those limits are exceeded; in these cases also it is only natural to suppose from our present knowledge that at a certain temperature one crystalline modification exists, the molecules of which are arranged in a certain definite manner, and that as the temperature drops the structure contracts, the molecules shrink nearer together, until ultimately when the temperature of change is reached, the structure jams and the same molecules arrange themselves anew in quite a different manner. When one polymorph changes into another

we do know that the point-system or structure changes, but we do not know that the unit of the structure alters at the same time; and since the change of point-system or of arrangement of the molecules is sufficient to explain all the facts, it is an offence against the law of parsimony to assume that the physical molecule changes during the interconversion of two polymorphous modifications of a substance. It should, perhaps, be pointed out that capillarity determinations have shown that many substances have not the same molecular weight in both the liquid and the gaseous state, the free particles in the liquid being apparently aggregates of gaseous particles; whether these polymolecular aggregates persist in the solid state is not yet known, but it would seem that no complication of this kind should affect salts, these being, according to Crompton, monomolecular in the liquid state.

Although Tutton's purely crystallographic work indicates that in a number of cases the chemical molecule is identical with the physical molecule in the crystalline state yet it is not to be expected that our knowledge of the relative weights of these molecules will be in the main derived from arguments deduced from the measurement of series of crystalline salts; the investigation is of so laborious a character and the interpretation of the results so liable to error as to suggest that the methods of physical chemistry are likely to lead more rapidly and surely to the desired end. Nernst has indeed indicated a method which will probably be found of general applicability, and which depends on a remarkable property of chemically related crystalline substances. Two compounds when very closely related chemically are nearly always obtainable in crystal of almost, though usually not quite, identical form; the structures in which the physical molecules of two such substances are arranged are thus of the same pattern, and the compounds are said to be isomorphous. A striking peculiarity of isomorphous substances lies in their power of crystallising together from solutions containing them both, crystals being deposited which contain the two salts in varying proportion, depending on the composition of the



liquid solution; these mixed crystals are termed "solid solutions" by van't Hoff, partly because their properties are in the main means of the corresponding properties of the two crystalline salts composing them, in the same way that the properties of a solution of one liquid in another is in the main a certain mean of the corresponding properties of the constituent liquids. If two non-miscible liquids lie in contact with each other, and a third substance A soluble in both these liquids be added to the mixture, equilibrium is after a time set up in the following manner; the substance A distributes itself between the two non-miscible solvents in such a way that the ratio of the amounts of A dissolved in equal parts of the two solvents (the so-called partition-coefficient) is independent of the actual concentration, provided only that the concentration is not great, that the temperature remains constant, and that the molecular weight of A is the same in each of the two solvents. Should, however, the molecular weight be twice as great in one solvent as in the other, the partition-coefficient is not constant, but becomes constant if a particular term of the ratio is squared before calculating. This method of determining molecular weights is applicable not only to two liquid solvents in contact but also to a liquid solution in contact with a solid solution of the same substance; thus if a series of aqueous solutions containing the isomorphous salts, potassium chlorate and thallium chlorate in various proportions be caused to crystallise at a fixed temperature, mixed crystals are deposited of such composition that the proportion of potassium chlorate in the mixed crystals divided by the proportion of the same salt in the liquid solution in contact with, and therefore in equilibrium, with them is a constant, and thus independent of the actual proportions of the two salts present in either liquid or solid solution, provided that the potassium chlorate is not present in large proportion. It is hence evident that in the crystalline state potassium chlorate has the same molecular weight as in solution, and that, therefore, the physical molecule is identical with the chemical molecule in the crystalline substance. Several disadvantages embarrass the easy application

of the method ; it could not be expected to hold rigidly as concentrated solutions such as are frequently employed, and the electrolytic dissociation occurring in aqueous solutions introduces a complication which cannot always be successfully eliminated. There is little doubt that Nernst's work in this field opens the way to a most powerful method of determining the molecular weights of crystalline substances.<sup>1</sup>

These and many similar considerations seem to indicate that at present the only legitimate view concerning the matter is that the molecular weight is in general the same in both the liquid and the solid state ; there is thus a complete analogy not only between the molecular properties of gases and liquids on the one hand but also between those of liquids and solids on the other. But just as in cases of the former kind exceptions arise, the molecular weight not being the same in the gaseous as in the liquid state, so doubtless exceptional cases will be found to exist amongst the latter. Consider such cases of polymorphism as that of the diamond and graphite or of the red and yellow crystalline modifications of phosphorus ; these are frequently quoted cases of allotropy of which the generally recognised meaning is that it is merely polymorphism occurring amongst the elements. The differences between the diamond and graphite or between red and yellow phosphorus are far greater than those observed between ordinary polymorphs such as those quoted above ; it would therefore seem only reasonable to accept the view that such substances are not ordinary polymorphs but chemical polymerides just as oxygen  $O_2$  and ozone  $O_3$ , or acetylene,  $C_2H_2$ , and benzene  $C_6H_6$ , are polymeric substances. Again, it is known that the molecular weight of sulphur only corresponds to the formula  $S_2$  at temperatures high above its boiling point whilst near the boiling point the gaseous molecules are at least three times as large and

<sup>1</sup> Whilst this article was passing through the press, Dr. Andreas Fock published a valuable paper in which he shows, by applying the equilibrium method briefly described above to many pairs of isomorphous salts, that all the salts examined have the same molecular weight in the crystalline, as in the dissolved condition.



therefore probably have the composition  $S_6$ . Further, when sulphur is heated from its melting to its boiling point it undergoes a remarkable series of changes ; near the melting point sulphur is a fairly limpid straw-coloured liquid which does not change rapidly in colour or consistency until a temperature not far below the boiling point is reached, when it suddenly assumes a deep-brown colour and becomes so excessively viscous that the containing vessel may be inverted without the liquid running out. It is scarcely conceivable that a change of this kind can be due to anything but a change in molecular complexity ; and, since changes in molecular complexity certainly occur in gaseous sulphur and almost as certainly in liquid sulphur, it is very possible that the six or seven different polymorphous crystalline modifications of solid sulphur have not all the same molecular weight but that some are polymerides of others.

The physico-chemical investigation of crystalline substances may be confidently expected to yield brilliant results in that department of chemistry which deals with tautomerism occurring amongst organic compounds ; this subject is one which every organic chemist recognises as presenting great difficulties and some of the ablest physical chemists have for long past applied their most ingenious efforts to its study. Many organic compounds are known which do not behave consistently during the ordinary laboratory operations ; in some reactions they behave as if they had a certain constitution whilst in others they seem to possess quite a different constitution. Such substances are said to be tautomeric and are supposed to possess each of the two constitutions at different times, the conversion from the one molecular constitution to the other being very readily brought about. In certain cases two tautomeric compounds can be isolated and examined ; their investigation in the liquid state is, however, extremely difficult owing to the complication introduced by the tendency to interconversion. Two tautomeric forms, if in the solid state, should be much more easily investigated than if they were in the liquid condition, because in the former case the tendency to rearrangement of the atoms composing the molecule would naturally

be much less and because crystallographic methods could be used to ascertain with ease and rapidity which of the two substances was under examination ; up to the present, however, crystallographic methods have not been applied to the study of tautomerism.

Although our knowledge of tautomerism apparently has much to gain from crystallography, yet a protest is necessary against a highly reprehensible practice which has recently been adopted by a certain school of organic chemists. Large numbers of organic compounds exist in several polymorphous forms, and naturally enough there are amongst these substances some, the chemical behaviour of which can be equally well represented by two tautomeric constitutions ; in these cases it seems to have become customary to assign one constitution to the one crystalline modification, and a different one to the second modification. This has been done in such cases as that of benzoïn with apparently no regard to anything but the fact that two molecular configurations are possible, and that two polymorphous forms exist ; it need hardly be pointed out that such a method of creating new compounds is hardly likely to redound to the credit of organic chemistry.

Should the view advocated above, namely, that the physical molecules or the units of the structure of crystalline substances are in the majority of cases the chemical molecules, we hold the key to many problems which have hitherto successfully resisted all attempts at their solution. The close crystallographic relationships often existing between substances which are not isomorphous, but, nevertheless, are more or less closely related in a chemical sense, have always been amongst the most curious and interesting of crystallographic phenomena ; these analogies are termed morphotropic relationships, and have doubtless escaped notice in hundreds of cases owing mainly to the fact that the crystallographic examination of organic compounds has been usually entrusted to mineralogists, who, naturally enough, are not alive to the chemical interests at stake. Here, again, the recital of an actual case will best serve to exemplify what is meant by a morphotropic relationship.



Camphoric acid crystallises from acetone in large transparent tablets containing acetone of crystallisation, and having the composition  $C_{10}H_{16}O_4$ ,  $\frac{1}{2}(CH_3)_2CO$ , which can be considered as built up on three rectangular axes, the ratios of the lengths of which are  $a : b : c = 1.2386 : 1 : 1.7172$ . Camphoric anhydride, which is closely related chemically to camphoric acid, crystallises without acetone in tablets of very similar appearance; these have the composition  $C_{10}H_{14}O_3$ , and may be referred to the rectangular axes  $a : b : c = 1.0011 : 1 : 1.7270$ . The ratio of the axes  $c : b$  is almost the same in the two cases, so that many of the angles measured are nearly identical on both kinds of crystals; the crystals of both substances cleave readily along a plane perpendicular to the  $c$ -axis, and less readily perpendicular to the  $a$ -axis. In each case the optic axes lie in the plane perpendicular to the  $a$ -axis, the smaller optic axial angle is bisected by the axis  $b$  and the double refraction is negative in sign; finally both kinds of crystals are striated in similar ways and almost the same planes are developed on each. The resemblances between the crystals, notwithstanding the great difference in composition, are extraordinarily close and cannot be regarded as due to mere coincidence; they indicate clearly that one plane section of each structure is of the same pattern in the two cases but that there is no such similarity in other sections. Morphotropic relationships of similar natures to the foregoing are frequently discovered; they indicate not only that the kind of grouping of the molecules in the crystalline substances upon which they are observed is of a somewhat similar character but also support the view that the physical molecules in crystalline substances are in general identical with the chemical molecules. The information to be gained by the systematic study of morphotropic relationships is undoubtedly great and cannot fail to well repay investigation.

In the preceding pages an attempt is made to demonstrate that many of those problems of physical chemistry which are now so quickly coming to the fore are so closely interlinked with crystallographic phenomena that to study

the former without a knowledge and appreciation of the latter is to court failure. Further, it may be remarked that the very complications introduced into the molecular physics of solids by the fact of their possessing crystalline structure only strengthens the methods of investigation ; the highly differentiated nature of crystallographic phenomena in itself alone renders crystallography one of the most powerful instruments of research at the disposal of modern science.

The chemist has in the past always been curiously apt in seizing upon and applying to his subject any branch of physics which bears in the slightest degree on chemistry ; many departments of natural science which our predecessors would have classified as pure physics are to-day so well identified with chemistry that to exclude their consideration from chemical text-books would excite surprise. Has not the time come for the chemist to annex crystallography and to set it in its true position as one of the most promising and fascinating branches of physical chemistry ?

WILLIAM JACKSON POPE.



## GERMINATION OF SEEDS. I.—THE VITALITY OF DORMANT AND GERMINATING SEEDS.

THE term germination is mostly used to connote resumption of growth by dormant *seeds*; this restriction is neither etymologically nor physiologically defensible, and is now merely a tribute to custom. Germination connotes resumption of growth by any dormant part of a *plant*, for the rationale of this process is in all cases comparable, the particular case of seeds being merely one aspect of its deconnotation. This article deals only with the germination of seeds to avoid undue extension, and primarily with the 'vitality' of dormant seeds, since it is obvious that the former is a function of the latter.

*Resistance to time.*—Numerous statements have been periodically made about the 'longevity' of seeds; the majority are of little value from lack of detail or of sufficient positive proof. The most notorious are those concerning seeds from sarcophagi of Egyptian mummies. It is now generally acknowledged that no adequate proof of their germination has been produced, the reputed success of some authors having been rather due to duplicity of Arab vendors than genuineness of the seeds. Burgerstein (1) quotes experiments of Unger with indubitably genuine seeds. Corns of *Hordeum hexastichon* from the ruins of Thebes were tested; not one germinated. The same result was obtained with corns of *Triticum* out of tiles made of Nile-mud and straw from the Darhur-pyramid near Cairo. There is nothing extravagant in the idea that mummy-seeds may retain potential life, but there is no proof that this is so; indeed, C. de Candolle (2) states that the wheat was always sterilized apparently before introduction into sarcophagi though no authority is given for this statement.

That the treatment of this subject is not wanting in humour is evident from that which follows: A well was once sunk in the Lias of Shipston-on-Stour; the next year *Glaucium luteum* appeared on the rubbish from the

shaft. No *Glaucium* had previously grown in the neighbourhood. White (3) suggests "that they (the seeds) had possibly remained inert from the time when the deposition of the Lias took place, and upon their exposure to the atmosphere were recalled to life".—This is not only extravagant, but transcends imagination.

An interesting case of reputed 'longevity,' that lacks however positive proof, is one recorded by v. Heldreich in 1873. A heap of mine-refuse on Mt. Laurion in Attica, 3 m. deep, had been removed shortly before he visited the spot. On the recently exposed surface a *Glaucium* was found, which he did not hesitate to consider as a new species, *G. Serpieri*; *Silene Juvenalis* Del., hitherto unknown there, was also found. To account for their appearance, he suggested that they had been dormant under the refuse-heap since it was first placed there, at least 1500 years ago. De Candolle (2) quotes a statement of A. P. de Candolle, who germinated seeds of *Mimosa pudica* after these had been dormant sixty years, and one of Girardin, who succeeded with seeds of *Phaseolus vulgaris* (haricot), that had lain more than 100 years in the herbarium of Tournefort. It is further stated that in 1850 Brown sowed seeds from the collection of Sir Hans Sloane, of which they had formed part longer than 150 years, and caused them to germinate. The latter cases seem quite trustworthy; one might however object that the seeds had possibly been changed unknown to the experimenters.

Experiments of Peter (4) support the view that the sudden appearance of species hitherto unknown, when soil has been disturbed, is due to persistence of seeds of one vegetation dormant in the earth while later vegetations succeed and to their subsequent germination when conditions changed. He tried to find if soil holds seeds, if it be able to preserve their 'vitality,' as well as which species have seeds capable of remaining thus unputrefied. Soils were tested on the surfaces of which vegetation had not existed for a long time; present covering with wood was disregarded, since tree-seedlings admit of easy distinction and could be eliminated. Soils were chosen concerning which it was



accurately known, whether considerable alteration in constitution of the vegetation had ever occurred. Samples of earth were so taken as to diminish as far as possible the chance of introduction of seeds by various agents. For collecting earth spots in dense forests devoid of vegetation were chosen, chiefly in such as were known to have formerly been fields or meadows. For comparison samples were taken from primæval forests. Layers 8cm. deep were removed; this was done twice, and sometimes thrice, at the same spot. The cultures agreed well. In every test of soil formerly field-soil, the majority of seeds that germinated, at times all, were those of field-plants. The results with earth from forests previously meadows, or perennially forests, were analogous. The woods, primæval ones naturally excepted, had been planted twenty to forty-six years back; Peter concludes hence that the seeds had remained dormant, retaining 'vitality,' throughout these periods. This conclusion is as reliable as any deducible from experiments of this type, which are permeated with uncertainty.

Loss of 'vitality' with age has been recently studied by Burgerstein (1) in seeds of *Triticum* (*vulgare*?), *Secale cereale*, *Hordeum* (*distichum*?) and *Avena* (*sativa*?), aged one to ten years. *Hordeum* preserved 'vitality' best, *Avena*, *Triticum* and *Secale* following in order. Of seeds aged ten years, 70 to 90 per cent. germinated in the case of *Triticum*, *Avena* and *Hordeum*, 1 to 2 per cent in that of *Secale*.

Concerning the longevity of *Triticum*, Acton<sup>1</sup> mentioned that no seed of a sample aged thirty years germinated. This trial was hardly fair, as the mode of storage was not favourable to preservation of 'vitality'.

Naudin<sup>2</sup> adduced this year an old experiment of his; in 1872 he received a bag of dusty earth from the Sahara, from which he reared a *Helianthemum*. In 1895 he received seeds from Gabon enclosed in earth that weighed less than 1kg., but from which he obtained more than

<sup>1</sup> "Changes in the Reserve-material of Wheat on Keeping," Note, *Ann. Bot.*, 7, 1893, 383.

<sup>2</sup> "La longévité des graines," etc., *Bull. d. l. Soc. Nat. d'Acclim. d. France*, Feb., 1897.

twenty seedlings, the seeds of which had been in the earth unknown to the collector. These are the facts which he thinks sufficient to establish 'longevity' of the seed: but they prove little, if anything. No details as to precautions taken against subsequent introduction of seeds are given; even if the seeds were in the original earth, there is nothing to show how long they had been there.

Arthur<sup>1</sup> states that seeds of *Pyrus coronaria* can germinate after dormancy of twenty-three years. The evidence for this is as follows: A barn was built in 1859, the foundation of which was limestone laid on soil. In 1882 the barn was removed, and after twenty days the foundation also. When the bottom stone was raised, two small plants were found near the centre of the stone. He says that there seems no doubt that the seeds had been protected by the building for the twenty-three years, germination having been stimulated after removal of the barn by penetration of warmth and moisture beneath the foundation. No evidence is adduced that the seeds were not introduced by animals or otherwise, for which reason the statement is practically valueless.

Jodin (5) succeeded in germinating peas (*Pisum sativum*?) after dormancy of ten years. Ten were tested; two germinated normally, two abnormally.

Instances of 'longevity' are also given by Meehan.<sup>2</sup> In 1886 he had a few plants of *Lysimachia atropurpurea* in his garden. Next winter this spot was covered to a depth of several feet with earth, and evergreens were planted on it. In 1896 one evergreen was removed and shortly after a plant of *Lysimachia* sprang up at the bottom of the hole thus made. Since none had grown in the garden since 1886, he concluded that the seed had remained dormant ten years. In 1884 plants of *Antirrhinum glandulosum* were raised by him; next year the plot where they had been was covered with earth to a depth of several feet. On turning up the earth in 1894 to a depth of a few feet, one plant came up and flowered. It is very likely that these seeds had re-

<sup>1</sup> *Bot. Gaz.* 7, 1882, 88.

<sup>2</sup> *Proc. Acad. Nat. Sci. Philadelphia*, 1892, 374; 1894, 58.



mained dormant for ten years, but the evidence adduced is too inadequate to enable one to say with absolute certainty that it was so. The seeds might, for instance, have been introduced on a spade, or in many other ways.

The experiments that tend most strongly to prove 'longevity' in certain seeds are those of Girardin and of Brown. The seeds tested had in each case been part of a collection which there was every reason to suppose had not been disturbed, and the age of which was known. But there is no absolute certainty that the seeds had not been interfered with, and this doubt weakens the evidence. There is only one method for settling the question beyond contradiction; large quantities of selected seeds of many species should be collected at some recognised institute after careful previous treatment, and allowed to remain quiescent in a suitable place, to which no one could get access without being known to have done so. These seeds should be periodically tested and the results recorded. The research of Peter, although admirably conducted, only supports strongly the idea of 'longevity' of seeds.

That this 'longevity' is a function varying with the species, and even individual seeds, admits of no doubt. Burgerstein (1) found that deviations due to individual differences in seeds of cereals amounted to from 1 to 16 per cent. Moreover the degree of maturity at harvest-time and the aqueous content at the time of preservation are factors that influence considerably the 'vitality' of seeds.

*Resistance to water.*—The influence of oceanic agency in distribution of certain plants has been long known; this is, stated in other words, that it has been long known that certain seeds can withstand protracted immersion in salt water. The old experiments of Darwin (6) on this point are interesting. Seeds were placed in bottles with salt water made according to Schweitzer's analysis. The trial was fair, as algæ and marine animals lived long in the water. With Darwin's results are conjointly published some of Berkeley's. The latter tied up seeds in bags and immersed them in sea-water which was daily renewed; immersion lasted three weeks, but since the seeds were

'posted damp, and not at once unpacked, total immersion was practically a month. Some of Darwin's bottles were exposed to weekly temperatures of  $35^{\circ}$  to  $57^{\circ}$  F., others to daily ones of  $46^{\circ}$  to  $56^{\circ}$  F. Seeds were also immersed for six weeks at  $32^{\circ}$  F., the temperature rising slowly during the next six weeks to  $44^{\circ}$  F. But seeds thus tested did not seem to withstand the injurious effect of salt water better than those exposed to higher but variable temperatures. The total number of species tested by the authors was eighty-seven; of these twenty-three did not 'survive' immersion of twenty-eight days. *Capsicum* was most resistant, for thirty out of fifty-six seeds germinated after immersion of 137 days, whereas of those of *Apium graveolens* only 6 per cent. germinated after like immersion. Several seeds of *Atriplex* germinated after immersion of 100 days, but those of the dwarf kidney-bean and *Hibiscus Manihot* were 'killed' by immersion of eleven days. All other species tested fell between these two extremes. It is noteworthy that the majority of seeds tried were such as might be expected to resist salt water least, not belonging to littoral plants; indeed, several were garden varieties.

Hemsley<sup>1</sup> cites experiments of Martins and Thuret on this subject. The former tested ninety-eight species; a perforated box was employed with as many compartments as kinds of seeds, being attached to a buoy. After exposure of forty-five days the box was opened; forty-one kinds were rotten; of the apparently sound remainder, thirty-five germinated. Several of the latter were essentially littoral. Fresh samples of the resistant thirty-five kinds were immersed for ninety-three days; only nine withstood the trial. The conditions of these experiments were better than those of Darwin's. The experiments of Thuret, in which immersion lasted thirteen months, yielded similar results; seeds of ten species (it is not stated out of how many) germinated, several with more vigour than the controls.

Evidence adduced by Salter (7) tends to prove that seeds can bear prolonged submersion in fresh and salt

<sup>1</sup> *Challenger Report*, 1. 3, appendix 277.



water without injury. In 1843 the channels of Poole Harbour were deepened, the mud raised being deposited on the shore, covering several hundred square yards; a quay was made from the hardened mud: this was never used, and the surface was not disturbed. Early in next spring the surface exhibited abundant vegetation of character totally distinct from that of the flora of the neighbouring shore, containing plants that did not grow within many miles, and one probably foreign to the county. It seemed conclusive to Salter that the seeds must have been in the mud when deposited; he concludes that the seeds fell into two rivers that flow into the harbour, and were ultimately deposited in the channels. The evidence given supports this view strongly; if his hypothesis be accepted, the seeds must have evidently suffered prolonged submersion both in fresh and salt water without losing 'vitality'. But however complete this kind of evidence may be, it is never conclusive, and, as with all induction, can only approximate to truth on reiterated confirmation.

Salter's views are, however, supported by observations of White (3). Mud was dredged from the Avon-bed and the floor of the basins at Bristol by local officials; this was emptied into a disused quarry, the work being done by manual and mechanical agency only. About half an acre was thus covered to a depth of from ten to twenty feet. In next spring a profuse and varied vegetation appeared; many of the species were native on the banks of the Avon above and below Bristol, but had not been found previously at or near this spot. There were also species recorded to grow in the Avon valley, but which had become extinct or extremely rare, as also others not noted before in the district, and some from all quarters of the globe. After comparing all the evidence at his disposal, White concluded that the seeds had been in the mud. This view is as justifiable as that of Salter's, and is open to the same objections. Some seeds may have lain long in the mud, others but a short time; there is no means of settling in any case the duration of submersion, and a safe criterion of judgment as to their origin does not and, moreover, from the nature of the case, cannot exist.

Guppy (8), after study of the agency of the Thames and Lea in the dispersal of plants, adopts similar views. It is said that, speaking generally, all seeds and fruits in the drift of spring have floated through winter ; this statement is not merely based on their occurrence in the spring-drift, but also on a series of control experiments. Germination may be delayed till the next year, seeds of *Iris pseudacorus* having germinated afloat after immersion of fourteen months ; growth in spring had been stopped by placing the seeds in a cool place. There are scarcely any seeds and fruits common in the drift of these rivers that will not float for months in sea-water and germinate afterwards. Fruits of *Sparganium ramosum* germinated after flotation of twelve months in sea-water. Those of several species 'survived' immersion of three to five months, their limit of buoyancy not having been then reached. Fruits of three species germinated after immersion of months in sea-water, the density of which had been raised to 1.05 by addition of salt ; the average density at 0° C is 1.02975.<sup>1</sup> Some seeds, as those of *Lemna minor*, only resist flotation of a few days. It is further stated, and this is important with regard to the observations of Salter and White, that sinking of seeds need not involve loss of 'vitality'.

Ewart (9) mentions that immersion of seeds of peas (*Pisum sativum* ?) for five days in water reduces the percentage of germinating seeds to 60 per cent. ; this fell to 0 per cent. after immersion of fourteen days. With *Phaseolus vulgaris* (haricot) the latter percentage is reached after ten days, with *Triticum (vulgare ?)*, *Hordeum (distichum ?)* and *Linum usitatissimum*, after three weeks, whereas 17 per cent. of seeds of *Cannabis sativa* germinated after exposure of four weeks. These experiments contravene distinctly those of Guppy ; this is perhaps explicable on the assumption that in this case not dormant but germinating seeds were killed : at all events this is supported by the conditions and results of the experiment.

Horticulturists have long known that steeping seeds in hot water accelerates and augments their power of germina-

<sup>1</sup> *Treatise on Chemistry*, Roscoe and Schorlemmer, i., 266.



tion. Wernicke<sup>1</sup> has examined the action of hot water on various seeds that germinate slowly owing to thickness or impenetrability of their integuments. Seeds of *Acacia molissima* and *Lathyrus sylvestris* were kept in hot water and then allowed to germinate. Of the controls 50 per cent. germinated. The following table gives the results :—

Period of Immersion.	Temperature.	Percentage.
6 hours.	50°C.	60 per cent.
3 „	80°C.	72 „
1 „	95° – 100°C.	92 „

Observations of considerable interest on the action of water, and of air saturated with water, at different temperatures occur in a paper by Just (10); limitation of space precludes more than indication.

*Resistance to thermometric extremes and desiccation.*—But little work has been done on the influence of intense cold on the ‘vitality’ of seeds. The earliest seems to have been that of Edwards and Colin quoted by Wartmann (11); seeds of cereals were subjected to a temperature of  $-40^{\circ}\text{C}$ . for some minutes, produced through evaporation of sulphur-dioxide in vacuo. Germination occurred as in the controls. There is a serious objection to this experiment, namely, that the duration of exposure was insufficient to allow the seeds to reach the temperature quoted. Wartmann (11) tested nine species; the seeds were divided into three lots; one served as a control, the second was placed in a thin glass tube, that was hermetically sealed and refrigerated for half an hour at  $-57^{\circ}\text{C}$ . in a bath of sulphur dioxide: the tube was finally plunged into a mixture of snow and salt, where it remained fifteen days exposed to the winter cold. The third lot was also enclosed in a glass-tube and placed at first inside a metallic receiver, in which was liquid carbon dioxide, that on solidification produced a temperature of  $-78^{\circ}\text{C}$ . The tube was then covered with paste of solid carbon-dioxide and sulphuric ether and placed

<sup>1</sup> Abst. *Ann. Agron.*, 21, 1895, 544.

in vacuo; the exposure lasted more than twenty minutes, and the temperature sank to  $-110^{\circ}\text{C}$ . Every seed germinated. It might be reasonably urged that exposure was here also inadequate for the acquisition of this low temperature by the seeds. A further communication appeared later (12); seeds of *Æsculus Hippocastanum* were wrapped in the tin-foil and placed in a paste like that mentioned above, in vacuo; exposure lasted two hours and the temperature was at least  $-110^{\circ}\text{C}$ . Germination occurred as in controls. This experiment yields doubtful results; the seeds may, or may not, have acquired the temperature in question throughout. De Candolle and Pictet (13) utilised liquid sulphur-dioxide and nitrogen-monoxide as refrigerating agents. In their first experiment four tubes of thin glass, each enclosing seeds of the same species with metallic fragments, were hermetically sealed and placed in a test-tube, that was also hermetically sealed. The latter was covered with tow, which was constantly sprinkled with sulphur-dioxide, and exposed to air. The tube was thus submitted to gradual lowering of temperature from  $-39^{\circ}\text{C}$ . to  $-50^{\circ}\text{C}$ . for six consecutive hours. All seeds of three species germinated as in the controls. Of twenty-four seeds of *Triticum* (*vulgare*?), only seven germinated, but the authors attribute this to an accident. In their second experiment thirty species were tested. When  $-40^{\circ}\text{C}$ . had been reached, nitrogen-monoxide was poured several times into the tube with the seed-tubes. At the close of the experiment that lasted two hours the temperature was  $-80^{\circ}\text{C}$ ., which was supposed to have obtained for at least an hour. No precautions were taken to graduate thawing, and the seeds were not previously desiccated. Every lot, among which was *Triticum*, germinated except three, in which cases the controls also refused to germinate. The first experiment is probably reliable; the second is dubious on account of shortness of exposure. In a subsequent paper (14) seeds of several species were kept for four consecutive days at a temperature lower than  $-100^{\circ}\text{C}$ ., obtained through evaporation of solid carbon-dioxide. Germination was normal in four lots; in four others it did not occur, as also in the



controls. This experiment is important being the first wholly reliable one; there can be no reasonable doubt but that the seeds acquired the temperature throughout. More recently Pictet (15) says that he subjected seeds to  $-200^{\circ}\text{C}$ . in liquid air, and that development succeeded as in the controls. This statement loses much importance through absence of detail, not even the duration of exposure being given. These experiments are in very important relation to the question of the 'vitality' of seeds.

Yet more recently De Candolle (2) gives results of an exposure of 118 days at an average but intermittent temperature of  $-41.93^{\circ}\text{C}$ . The species tested were *Triticum* (*vulgare* ?), *Avena* (*sativa* ?), *Fœniculum officinale*, *Mimosa pudica* and *Lobelia Erinus*. Those of each species were enclosed in capsules of tin-foil which were placed in a sheet-iron box, which was completely filled; the box was soldered and enclosed in a wooden case, that covered all surfaces but one. This was done to preclude injury, for cooling occurred in the refrigerator of a firm of importers of frozen goods. The covering was proved to exert no serious influence on cooling. The cooling agent was cold air. During the experiment refrigeration lasted eight to twenty hours *per diem*; the minimal temperature recorded was  $-53.89^{\circ}\text{C}$ ., the maximal  $-37.78^{\circ}\text{C}$ . After cooling the temperature assumed that of the recipient; it is doubtful if this ever reached  $0^{\circ}\text{C}$ . Almost all seeds of *Triticum*, *Avena* and *Fœniculum* germinated normally, but only thirteen out of sixty seeds of *Mimosa*. Out of a large number of *Lobelia*-seeds only ten germinated. With *Mimosa* inhibition was not in all cases due to cold, since many seeds in the controls did not germinate; this could not however be said of *Lobelia*. This experiment is important on account of its long duration, no similar one having ever before been made.

Hart<sup>1</sup> mentions that seeds planted under shelter of glass ashore in Discovery Bay germinated and grew; when the sun was at greatest altitude the temperature within the glass was raised one or two degrees, but that

<sup>1</sup> *Jour. Bot.*, 1880, 74.

inside and outside was mostly uniform and constantly as low as 33° F. (presumably - 33°). The excessive cold of winter months, involving upwards of 100° of frost, is also not fatal to mature seeds. Grains of *Triticum* left at Polaris Bay during Hall's expedition, which had lain entirely exposed to the weather for four successive years, germinated in Discovery Bay. Beans (*Faba*?) and peas (*Pisum*?) that germinated had suffered the whole severity of winter on deck with a minimal temperature of - 71° F.

Kerner v. Marilaun<sup>1</sup> cites that the mean temperature of January at Jakutsk and Werchojansk in Siberia is - 42.8° C. to - 49° C., and that - 62.0° C. and - 63.2° C., the lowest temperature ever noted on the earth, have been recorded there. Here also for months the shade-temperature is never above - 30° C.; yet not only do seeds germinate when the conditions become favourable, but plants persist and live.

Guppy (8) shows that enclosure in ice of an English winter does not affect the 'vitality' of seeds enclosed.

Concerning resistance to high temperatures Just<sup>2</sup> states that seeds of *Trifolium pratense* withstand temperatures up to 120° C., if previously desiccated and kept so during the experiment; exposures were from half an hour to two hours. Subjection to high temperatures always involves slower and more imperfect germination than that to lower ones. The more complete the desiccation is, he adds, the less is the injury, but that most careful desiccation will not prevent notable harm with temperatures over 100° C. Later Just (10) experimented partly with carefully desiccated seeds. Dehydration was effected by exposure to sulphuric acid for two days, then in a closed tube to calcium-chloride for ten days at room-temperature; subjection to high temperatures took place in the tube. *Hordeum* and *Avena* were tested. If the tubes were placed in the thermostat at once, the seeds of *Hordeum* were almost killed, those of *Avena* considerably damaged; if, however, they were gradually taken to 100° C., thus effecting a more

<sup>1</sup> *Pflanzenleben*, vol. i., 508.

<sup>2</sup> *Bot. Ztg.*, 1875, 52. Quoted in Just's paper (10) of bibliography.



complete dehydration, the injury was less, and the slower the ascent, the less the harm. At  $110^{\circ}$  C. the injury was more pronounced; half an hour at  $122^{\circ}$  C. 'killed' 99 per cent. of corns of *Hordeum*, whereas those of *Avena* withstood exposure of three hours. The fatality was always increased with the duration of exposure. Above  $122^{\circ}$  C. all seed were 'killed'.

It is curious that resistance to high temperatures is so modified by the aqueous content of seeds, as these and other experiments show, while that to low ones is unaffected, as De Candolle and Pictet have shown.

In Just's paper, results obtained by Haberlandt are quoted which show that desiccated seeds resist exposure of forty-eight hours at  $100^{\circ}$  C.; these results were confirmed by Krassan.

The results of van Tieghem (16) on this subject contradict those of almost all other observers; it was found that if fruits of cereals were dried at  $100^{\circ}$  C. till no further loss of weight ensued, 'vitality' was completely destroyed. The contradiction is difficult to explain; that the seeds were not completely dehydrated seems certain, for it is known that certain carbohydrates can be reduced to constant weight at  $100^{\circ}$  C., and yet yield more water without decomposition at higher temperatures.

It will not perhaps seem out of place to emphasise once more the undoubted fact, that one cannot speak of a constant specific, or even individual, resistance to environment; variation in origin and treatment affects the 'vitality' of seeds correspondingly.

Goff found that seeds of *Triticum* (*vulgare*?) and *Zea Mays* could be germinated six and five times respectively, when the periods of germination were separated by intervals of desiccation for seven days. Van Eyck,<sup>1</sup> who quotes this, obtained like results; seeds that had germinated were removed every twenty-hours and submitted to dehydration in an exsiccator for a week: these operations were repeated till the power was lost. The accompanying table gives his results:—

<sup>1</sup> De la germination répétée des graines, *Ann. Agron.*, 21, 1895, 236.

Species.	Period of Desiccation.	Frequency of Germination.
<i>Triticum (vulgare?)</i>	101 days.	14 times.
<i>Zea Mays</i>	35 "	6 "
<i>Raphanus sativus</i>	28 "	5 "
<i>Pastinaca oleracea</i>	14 "	2 "
<i>Daucus Carota</i>	" "	" "
<i>Trifolium sp.</i>	" "	" "
<i>Apium graveolens</i>	7 "	1 "

Seeds that germinated first always supported interruption best; the effect of the latter was almost always ramification of the radicle and annihilation of its geotropism.

Ewart (9) made somewhat similar experiments with peas (*Pisum?*), to see the effect of alternate steeping and drying. The seeds were spread on blotting-paper, and left to become air-dried. Only one experiment was apparently made, involving three interruptions. If the integuments remained entire, the effect was more fatal than if visible germination had commenced. Irregular development of radicles was noticed. The 'vitality' of radicles was found greater than that of plumules, and often the cotyledons showed more resistance than both.

That seeds offer considerable resistance to desiccation is obvious from study of the prevalent conditions in torrid districts. Kerner v. Marilaun<sup>1</sup> states that the highest temperature noticed in superficial soil of the earth was at Chinexo on the Loango Coast near the equator. Here 75°C was frequently exceeded, 80°C was often reached, and once 84.6°C; annuals, however, grew on entrance of the rainy season, the seeds of which had doubtless remained in the soil for months.

*Resistance to chemical agents.*—A few years ago a research of considerable interest by Cornevin (17) appeared, bearing on the toxic influence of alkaloids on plants. The incentive to the work was given by the theory of dependency of immunity in animals on production of antitoxines. He examined: (i.) the action of the poison of a species on its own seed, (ii.) that of the same poison on seeds of differ-

<sup>1</sup> *Pflanzenleben*, vol. i., 518.



ent species, and (iii.) the physiological reaction between seeds and different poisons. The first case presented two aspects: (i.) that in which the poison exists in the seed and passes into the seedling by a 'kind of heredity,' there being no interruption of the poisonousness of the plant, and (ii.) that where the poison exists neither in seed nor seedling, but is formed later. For the study of the first aspect, *Agrostemma Githago* and *Cytisus laburnum* were chosen, yielding respectively saponine and cytisine. To obviate the objection that the poison did not penetrate, the integument was always removed throughout the research. Neither 'death' of the seeds nor retardation of their germination occurred. For examination of the second aspect, *Nicotiana tabacum* and *Papaver somniferum* were used; the former yields nicotine in the leaves, the latter opium in the capsules. Two experiments on different lines were arranged with nicotine; the first proved that, without actual 'death,' germination was retarded: the second showed that germination cannot occur, or with great difficulty, in a medium impregnated with nicotine. Curiously enough it was found in the case of *Papaver*, that opium excites the power of germination. The isolated action of the best-known opium-alkaloids was then tried; these were morphine, narceïne, codeïne, papaverïne, narcotine and thebaine, all as hydrochlorates. Narcotine, codeïne and narceïne acted as opium; morphine and thebaine seemed indifferent, whereas papaverine had an inhibitory action.

In the study of the second of the above-mentioned cases, the action of oleandrine from *Oleander* and andromedotoxine from *Azalea* was tried; these, highly poisonous to man, were here in most cases inoffensive. It is interesting to note that *Phaseolus vulgaris* (haricot) was unaffected by oleandrine, but retarded in germination by andromedotoxine. Colchicine proved harmless in several cases, but affected *Phaseolus vulgaris* seriously; similarly with cytisine. This plant is thus seen to be extremely sensitive to toxic agents, and Cornevin correlates this sensitiveness with that to cold, which precludes its cultivation in northern countries. This sensitiveness is, however,

evinced in many other ways, as Ewart's experiments, and those of others, show.

Examination of the third case mentioned above demonstrated that resistance to these poisons is lessened as duration of exposure to their influence is lengthened.

The question of the effect produced on seeds by deprivation of oxygen was the subject of an important communication by Romanes (19). The method adopted consisted in sealing up seeds in vacuum-tubes of high exhaustion, in which they remained fifteen months; in other cases, after rest of three months in vacuo, seeds were transferred to other tubes charged respectively with various gases at the atmospheric pressure of the time of sealing. After a further period of twelve months the seeds were sown. The gases employed were carbon-dioxide and -monoxide, oxygen, hydrogen, nitrogen, hydrogen-sulphide, water, ether, chloroform. In all cases (with one exception) the seeds were weighed individually, and seeds of equivalent weight were taken from the same original packets as controls. The results proved amply, that neither a vacuum of  $1/1,000,000$  of an atmosphere, nor any of the gases, exercised much, if any effect on the 'vitality' of the seeds. Germination was in all cases perfectly normal. These experiments prove conclusively that dormant seeds do not respire.

Confirmation of Romanes' results are not wanting; similar ones have been obtained by De Candolle (2), Jodin (5) and Ewart (9) as regards the effect of deprivation of oxygen. The first enclosed seeds in a capsule of metallic foil, to which a wire of platinum was attached; the capsule was plunged under mercury, and frequently agitated to remove bubbles of air adherent to the seeds. If respiration occurred, it could be only due to air contained in the seeds before immersion. The results of four experiments showed that this treatment did not affect the 'vitality' of the seeds. In two of Jodin's experiments seeds were introduced into a bent receiver full of air, which was inverted under mercury; the whole was kept in a dark cupboard, in one case for four years, seven months and six days, in the other for three years and seven months. The air was then



analysed and the seeds tested in the first case. In the first experiment the composition of the air had been practically unchanged; every seed germinated. In the second some oxygen had been absorbed and some carbon-dioxide formed, but the amount was small. In a third experiment twenty peas (*Pisum*?) were introduced into a test-tube filled with mercury, and inverted over this liquid. No gas was noticed at the beginning or end of the experiment. After 4·5 years, ten peas were placed to germinate; eight developed perfectly, two refused. At the end of ten years and three months the remainder were removed; two germinated normally, two abnormally, and six not at all. Thus peas remained more than ten years in mercury-vapour of feeble tension without respiring, and yet preserved 'vitality' to a certain extent. For the study of this question Ewart placed seeds in corked bottles with an open erect tube containing clean pieces of sodium; the tube was then hermetically sealed. The atmosphere soon consisted of hydrogen and nitrogen. After three and five weeks the seeds were tested. Resistance, which was considerable, varied with the species. This experiment is also of interest, since it measures the resistance of the seeds employed to desiccation.

Van Tieghem and Bonnier (20) have obtained results discordant with those mentioned above. Samples of seeds were divided into three equal parts, each having the same number of seeds of the same species. One lot was placed in a cardboard box, into the interior of which air had free access; the second was placed in a glass tube full of air, which was then carefully corked and submerged under paraffin at the corked end: the third was put into a test-tube full of mercury which was then filled with carbon-dioxide. The seeds had been previously weighed. Each tube was submitted to like conditions for two years. All the seeds left in the open air had increased in weight by the close of this period; those in closed air had done so very slightly, whereas those in carbon-dioxide had not altered their weight. Germinating power was highest in the seeds left in the open air, much less in those kept in the closed air, whereas those previously in carbon-dioxide failed to germinate in every

case. The closed air had in the tubes of two out of four species suffered considerable alteration. The increase in weight of the seeds is attributed to metabolism. Since the authors tested only four species and made but few experiments with them, whereas Romanes made most careful trial of nine, and several series of experiments, it is more probable that the results of the latter are more accurate; further, they are confirmed by those of Ewart, De Candolle and Jodin, whereas those of van Tieghem stand isolated.

The action of vapour of ether, chloroform, alcohol and acetic acid on dormant seeds was also tried by van Tieghem and Bonnier. Seeds of five species were suspended in a flask containing the liquids; after introduction of the seeds, the flask was hermetically sealed. Exposure of four hours reduced the percentage of normally germinating seeds and retarded development; exposure of four days accentuated the results, while more prolonged action destroyed 'vitality'. The integuments were shown to afford enormous protection. The former results contradict again those of Romanes.

De Bary<sup>1</sup> has stated that seeds of *Lepidium sativum* withstand immersion of a month in absolute ethylic alcohol; Ewart (9) has confirmed this, but finds that 'vitality' is lost after exposure of five weeks. Peas (*Pisum*?) endured immersion of seven to nine weeks without losing the power of revival in all cases; immersion of nine weeks however annihilated this. Seeds of *Cannabis sativa* lost the power in one day, those of *Linum usitatissimum* and *Triticum* (*vulgare*?) by five weeks; those of *Hordeum* (*distichum*?) by seven weeks. Fifty per cent. alcohol destroyed the 'vitality' of these seeds in one day; those of peas (*Pisum*?) withstood 90 per cent. alcohol better than both preceding percentages. The seeds mentioned above lost 'vitality' after immersion of one day in aqueous solution of mercuric chloride (percentage not given); peas (*Pisum*?) however withstood it in alcoholic solution from three to six weeks.

<sup>1</sup> *Lectures on Bacteria*, p. 63. Quoted by Ewart.



Experiments were also instituted to ascertain whether dormant seeds respired ; air deprived of carbon-dioxide was aspirated over peas and then through an aqueous solution of barium-hydroxide for ten to fifteen days : no trace of carbonate was formed. This is a further refutation of van Tieghem's statements.

The action of twenty-two salts on the ' vitality ' of dormant grains of *Triticum (vulgare ?)* has been studied by Bruttini<sup>1</sup>; the grains were immersed for twenty-four hours in 1 to 2 per cent. solutions : considerable difference in inhibitory action resulted.

Similar experiments have been made by Vandeverde,<sup>2</sup> who steeped seeds in various solutions for twenty-four hours and then placed them to germinate. Every solution influenced germination. He intends to publish shortly an extensive communication, embodying the results of his own work and that of others.

Mosso<sup>3</sup> finds that alkaloids exert a narcotic or stimulating action on germinating seeds according to the concentration of the solution employed. Seeds were germinated in solutions containing from 0.00001 to 2 per cent. of the hydro-chlorates of morphine, nicotine, cocaine, of the sulphates of strychnine and atropine, and of caffeine salicylate.

*Retrospect.*—Exigence of space forbids more than a short critique of the more important questions raised on comparison of the preceding pages. One point towers above all others, namely, that of the ' latent life ' of dormant seeds. Pictet has stated that no chemical action occurs at  $-100^{\circ}$  C., and Dewar has undoubtedly shown that it is unknown with one or two exceptions at from  $-182^{\circ}$  C. to  $-192^{\circ}$  C. ; yet seeds kept for four consecutive days at  $-100^{\circ}$  C. germinated, and still more such as had been exposed to nearly  $-200^{\circ}$  C. Further, Romanes, Ewart and De Candolle have shown that seeds, that have not respired for more or less long periods, retain ' vitality '

<sup>1</sup> A. Bruttini, *Ann. Agron.*, 21, 1895, 542.

<sup>2</sup> A. J. J. Vandeverde, *Chem. Centralb.* 1897, p. 822.

<sup>3</sup> U. Mosso, *Ann. Agron.* 21, 1895, 544.

still, while JODIN proved that this is also true when respiration has been completely inhibited for years.

Are, then, dormant seeds alive, or are they dead?—The most perfect definition of life is probably that of Herbert Spencer,<sup>1</sup> who defines it as “the continuous adjustment of internal relations to external relations”. Now dormant seeds may be subjected to most varied environment, the factors—temperature, hydration, time, etc.—undergoing enormous variation, and yet remain absolutely inert; there is no evidence of adjustment of internal relations to external relations. If this definition be accepted no life, whether latent or weakened (*valentie*), can be attributed to dormant seeds. It is possible however that some may hold that, in the light of present knowledge, this definition becomes untenable, and that an extension is necessary. This amendment is not however practicable; for if Spencer’s definition were so modified or extended as to comprehend the state of dormant seeds, all definitions of life must become self-contradictory, and consequently all definitions of protoplasm, which have for the most part but the one postulate of life in common, would then in addition become self-contradictory, for it would be impossible to combine in a definition the qualities of the cell-contents of a resting seed, on the one hand, with those of protoplasts on the other, since they are perfectly antithetic. It must be hence granted that dormant seeds are not alive.

Are they then dead? — Weismann’s<sup>2</sup> definition of death, “der unwiderbringliche Verlust des Lebens eines Organismus,” is excellent, provided that the nature of life is fixed. By substituting Spencer’s definition of life for the word life, two harmonising definitions of life and death are obtained, which are probably more perfect than any others. Now it is a truism that many dormant seeds germinate when placed in suitable conditions,—hence, these are not dead.

What state then is this, that is neither life nor death?—As a matter of fact life in all dormant seeds is completely

<sup>1</sup> *Synthetic Philosophy; Principles of Biology*, London, 1884, vol. i., p. 80.

<sup>2</sup> Aufsätze über Vererbung, Jena, 1892. *Ueb. Leben und Tod.*, p. 131.



arrested ; in some cases potential life is retained, in others it is lost. For the sake of illustration the former state may be compared with that assumed according to Buddhistic philosophy by an individual consequent upon his entering Nirvâna ; once here all individuality is annihilated : the state is existence without a single attribute of life. There is however one essential difference between this state and that of the dormant seed ; an individual after entrance into Nirvâna has lost even potential individuality, but the seed retains this. In the case in which seeds have lost potential life, death obtains. It is at present impossible in most cases to distinguish between these two kinds of seed in the naturally desiccated condition, no matter what agents be invoked, except by testing the power of germination. That there is a chemical, probably also a physical, difference is obvious ; the difference may be only slight, but it suffices to determine whether resuscitation is possible or not.

It seems physiologically necessary to distinguish verbally between this state of dormancy and that of life, on the one hand, and death on the other. This can be adequately done—as I venture to suggest—by the term *hypnosis* ; the corresponding adjective is *hypnotic*, and the substantive, *hypnote*. The cell-contents of a *hypnote* would then be *hypnoplasm* ; *hypnospore* and *hypnosperm* are already recognised phytological terms, and experiments of Pictet have justified their existence, for he has found that these spores are still *hypnotic* after exposure to a temperature at which no chemical action is possible. It is true that some of these terms have a different connotation in psychology, but this need not militate against their employment in phytology. The homologue of *hypnoplasm* in dead seeds, etc., may be termed *necroplasm*, corresponding with the established term *necrosis*. *Bioplasm* as an equivalent for *protoplasm* has long ago been coined by Beale.

The protoplast has often been compared with a machine ; this simile has been as often declared inappropriate. DE CANDOLLE (2) has indeed shown that, as regards ordinary machines, this is an inefficient comparison ; the same has

been more completely demonstrated by Spencer.<sup>1</sup> It is distinguished by one essential quality, irritability, from all known machines. But, on the other hand, the protoplast as a phenomenal object can only be an instrument for transmission and transformation of energy, that is, a machine. How can this apparent paradox be explained?—The solution is not difficult. The term machine is always used to denote an instrument for transmission and transformation of energy, the nature of which is more or less perfectly known; but in the protoplast processes occur concerning which practically nothing is known. It is these difficulties that form the stumbling-blocks over which so many fall; inability to appreciate the protoplast as a machine is merely a phase of mysticism. The phytologist that refuses to recognise the protoplast as a machine errs similarly to the savage who attributes life to a watch, because the mechanical processes manifested in this machine are not recognised by him as identical in essence with those of more simple machines with which he is acquainted. The one makes an animal out of the watch, the other a god out of the protoplast.

It is not to be inferred that a form, or forms, of energy differing from any at present known may not be manifested in the protoplast; that may be so, or not. All that can be now said on the subject is: That the protoplast is a highly complex machine, and moreover an automaton, differing from all known machines, and that the rationale of its functionation is for the most part unknown. Pictet (15) says with perfect justice that life is a manifestation of natural laws, of the same type as gravitation. But he errs in stating that life is one of the constant forces of nature, if he intends to denote thereby that life is a single action comparable with gravitation; this may be so, but present knowledge is too insufficient to allow even condonation of such dogmatism.

Thus the protoplast is an automaton in action, the hypnoplast one at rest, and the necroplast one, the organisation of which has suffered irreparable injury. Also,

<sup>1</sup> *Loc. cit.*, chaps. iv., v.



organisms can assume one of three states—biosis (life); hypnosis (trance): necrosis (death).

The evidence with regard to 'longevity' in hypnotic seeds is very incomplete. Giglioli has suggested that these, after perfect desiccation are immortal; this is perfectly unwarranted, for, up to the present, no seed—as far as I am aware—has been ever completely desiccated. That ordinary hypnotic seeds with the average determined aqueous content of 10 to 12 per cent. are not immortal, is a truism. JODIN explains loss of hypnosis by intramolecular changes, analogous to those which occur in amorphous substances on becoming crystalline in lapse of time, without the aid of external energy. There seems no objection to this view.

In conclusion it may not be considered highly irrelevant to deprecate most strongly the laxity displayed by many phytologists in their methods of nomenclature. Plants are frequently specified as peas, beans, etc., a procedure that detracts very considerably from the value of their work. A pea, for example, may belong either to the genus *Pisum*, or to *Lathyrus*; also, a bean may either belong to *Vicia* (*Faba*) or *Phaseolus*. Such terms hardly beseem pages of a modern horticultural periodical, *a fortiori* those of a scientific one.

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






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ERUPTIVE ROCKS.

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## THE GEOLOGY OF MEXICO.<sup>1</sup>

IT is an encouraging sign of the times that the Republic of Mexico has recently established a geological survey; and it is still further matter for congratulation that the survey has already proceeded so far that it has been able to issue a sketch of the geology of the country as a whole. The sketch, no doubt, will require considerable alteration in the future; and, indeed, it is apparent upon the face of it that the palæontological evidence has not yet been sufficiently examined. But there is no reason to doubt its general accuracy, and it gives a very good idea of the geological structure of the Republic.

In a broad and general way the geology of Mexico offers some resemblance to that of the Peninsula of India. There is the same almost entire absence of fossiliferous Palæozoic rocks. The Trias contains little but plants, and the Jurassic is very feebly developed. At the close of the Cretaceous period there began a great series of volcanic eruptions, comparable with the Deccan Trap; but in Mexico these eruptions have continued down to the present day. In Mexico, too, the marine Cretaceous is much more extensively developed than in India.

Geographically, Mexico consists of a great central table-land, inclined towards the north and north-east, and included between two chains of mountains (the Sierra Madre del Pacifico and the Sierra Madre Oriental), which are separated from the sea by narrow strips of low-lying country. In the southern part of the republic the two chains unite with each other in the form of a V, near the apex of which are situated the great volcanoes of Popocatepetl, Ixtaccihuatl, Orizaba, etc.

South of the V, the country is lower, with a range of mountains parallel to the Pacific coast.

<sup>1</sup> Jose G. Aguilera. "Sinopsis de geología Mexicana. Bosquejo geológico de México: segunda parte." *Bol. del Inst. Geol. de México*. Nums. 4, 5, y 6, pp. 189-270. One map. Mexico, 1897.

Geologically, the rocks which occur in Mexico, may be divided into three distinct groups. First, we have the ancient crystalline and schistose rocks, which are presumed to be of Archæan age ; secondly, the sedimentary deposits, which extend from the close of the Palæozoic era to the present ; and lastly, a great series of volcanic rocks, which are mostly of Tertiary and Quaternary age.

The crystalline rocks constitute a great mass, which occupies a large part of the country at the southern angle of the V formed by the great mountain chains. They extend also for some distance along the western coast, and form a considerable part of the hills of the Sierra Madre del Pacifico in the state of Sinaloa.

The sedimentary deposits are much the most extensive of the three groups. They cover the northern, central, and eastern parts of the country, and also the southern extremity. None have been proved with certainty of earlier date than the Carboniferous, and neither these nor the Trias nor Jurassic are found except in isolated patches. By far the greatest space is occupied by Cretaceous rocks, which form nearly the whole of the Sierra Madre Oriental, and also a large part of the central plateau, where, however, they are often concealed by Quaternary deposits.

The volcanic rocks form nearly the whole of the Sierra Madre del Pacifico, and in the latitude of Mexico and Puebla they stretch almost across the width of the country.

#### ANCIENT CRYSTALLINE AND SCHISTOSE ROCKS.

The crystalline rocks, as already explained, form a large nucleus which occupies the southern part of the state of Puebla, some portions of the Sierra Madre in the state of Chiapas, and extensive areas in Oaxaca and Guerrero. Small scattered patches are also met with in the central plateau and elsewhere, while there is a large mass in Sinaloa. Crystalline rocks also form the axis of the mountain chain of the Californian Peninsula.

The rocks consist of porphyroid gneiss, gneissic and argillaceous schists, penetrated by veins of granite, granu-



lite, pegmatite, etc. Since no fossiliferous beds are known of earlier date than Carboniferous, it is evident that the age of these crystalline and schistose rocks is at best very uncertain.

#### PALÆOZOIC.

*Silurian*.—In the collection of the Institute there is a fragment of limestone displaying very fine specimens of *Orthis testudinaria*, Dalm; and this is stated to come from La Cuesta de Santa Teresa, one league (about two miles five furlongs) east of Cacahuamilpu, in the state of Guerrero. Several expeditions, however, have been sent, without success, to discover these deposits, and the occurrence must be considered doubtful.

Other rocks of various ages have been placed in the Silurian by various writers, but the correlation is in no case based on satisfactory palæontological evidence.

*Devonian*.—In the same collection there is a fine example of a Goniatite, which is referred to the Middle Devonian. The specimen is stated to have come from the ridge of Apulco; but here again subsequent expeditions have failed to discover any further specimens. It is believed, however, that certain schists below the Jurassic rocks of this neighbourhood may have yielded this fossil, and may really be of Devonian age.

*Carboniferous*.—The occurrence of Carboniferous rocks in Mexico has been definitely proved. They are found on the borders of Guatemala, where they contain *Productus semireticulatus*. The rocks are limestones and dolomites, passing down into sandy conglomerates.

Dr. Persifor Frazer has referred to the Upper Carboniferous the limestones which form some of the ranges in the states of Coahuila, and Nuevo Leon; and he bases this view on the identification of a certain number of fossils by James Hall and A. Heilprin. But the specimens are too badly preserved to be specifically identified, and even the generic determinations are open to doubt. From the results of other expeditions to these localities, the limestones are now believed to be the Cretaceous.

Other rocks which have been referred to the Carboniferous, have since been found in some cases to be of Cretaceous, and in others of Triassic, age.

#### MESOZOIC.

*Trias*.—The Trias appears at one time to have covered a considerable extent of country; but it is now visible only in a few scattered patches, of which the best known is perhaps that of Los Blancos in Sonora. The formation is also met with in Puebla and other states.

The beds consist of quartzose sandstones and argillaceous deposits. They are very variable in character and change not only vertically but also horizontally.

*Ceratites* has been recorded from the Sierra de la Encantada, in the state of Chihuahua; but this range is stated by Aguilera to consist of Cretaceous deposits.

The fossils which have been found are chiefly plants, and among these are species of *Gangamopteris* and *Macroptæniopteris*, genera which are characteristic of the *Glossopteris* flora of India and the southern hemisphere.

*Jurassic*.—The Jurassic rocks also are met with only in scattered patches, the largest of which occurs on the borders of Zacatecas and Coahuila. They consist of argillaceous marls and marly sandstones, covered by calcareous marls, and finally by limestones, which pass up quite conformably into the Cretaceous.

Fossils are abundant, but have not yet been closely examined. They include a considerable number of Cephalopoda. Most of the species are held to be distinct from those of Europe, but the most abundant are of Upper Jurassic facies.

*Cretaceous*.—The Cretaceous System, unlike the preceding, occupies a very considerable area. It forms the greater part of the Sierra Madre Oriental and covers most of the great central plateau, excepting where it is concealed by Quaternary deposits. It also occurs in large patches in the southern part of the Republic, south of the great plateau.



Palæontologically and lithologically it may be divided into three great subdivisions.

The Lower Cretaceous is composed of green argillaceous and marly rocks and calcareous and marly sandstones, covered by variegated clays. Sometimes it rests directly upon the crystalline rocks and sometimes upon the Upper Jurassic.

The Middle Cretaceous consists of grey, blue, or blackish limestones, which occasionally emit a foetid odour when struck with a hammer. This is much the most widely spread of the three subdivisions. It predominates in the north and east of the country and forms the greater part of the Sierra Madre Oriental. Sometimes it rests upon the Lower Cretaceous, sometimes upon the Upper Jurassic, and sometimes upon the Trias; and it has suffered much from folds and faults.

The Upper Cretaceous consists of light-coloured sandstones alternating with grey and blackish argillaceous deposits, which locally become more or less marly or calcareous. This division is not so much affected by folds and faults as the preceding, and frequently lies horizontally.

Towards the close of the Cretaceous period, or at the beginning of the Tertiary, began the great volcanic eruptions which form so striking a feature in the recent geological history of the country.

The fauna of the Cretaceous is remarkably rich and includes a considerable number of European forms. *Hippurites*, *Radiolites* and allied genera are met with; and *Ammonites* are abundant. The fauna of the middle division (which corresponds with the Cenomanian, Turonian, and a part of the Senonian) is naturally the most abundant, since this division is the most widely spread.<sup>1</sup>

#### TERTIARY.

The Tertiary deposits are found along the sea-coasts and also on the central table-land. In the former case they are marine, and in the latter lacustrine.

<sup>1</sup> I have not referred hitherto to the wealth of minerals in the various systems; but it is worthy of note that the Cretaceous Limestones are in places impregnated with cinnabar and other ores of mercury.

Among the oldest of the Tertiary rocks are those which succeed the Cretaceous in the valley of the Bravo (the Rio Grande) between Laredo and Guerrero. They consist of sands and marls, and belong to the Lower Eocene; and they are succeeded by marly sandstones which belong in part to the Eocene and in part to the Miocene.

In the Peninsula of California, especially upon the Pacific side, the coast is formed of sandstones and conglomerates, which consist largely of fragments of trachyte and andesite. These belong to the Upper Miocene and Pliocene.

In the low-lying country along the coast of the Gulf of Mexico, the Tertiary deposits form a band parallel to the shore, extending from the Rio Grande southwards beyond Vera Cruz, where they expand into a broad mass covering the greater part of the states of Tabasco, Campechi, and Yucatan. These deposits are marine in character and consist of shelly limestones and agglomerates. In the lower beds Miocene fossils predominate, while in the upper beds Pliocene and living forms are common.

Besides these, there are other deposits which must be referred to the Tertiary period. Thus, the lignite-bearing beds of Zacualtipan, in the state of Hidalgo, may be placed at the top of the Miocene or in the Pliocene; and numerous conglomerates formed of Cretaceous and other fragments are believed to be of Pliocene age.

But the most interesting of the Tertiary rocks are the volcanic lavas, agglomerates and ashes which cover so much of the country. The period of vulcanicity began with the ejection of syenites, hornblendic diorites, quartz diorites, and diabases, the age of which cannot be exactly determined, but is believed to be either late Cretaceous or early Eocene.

The next eruptions, which belong to the Miocene period, consist of andesitic porphyrites, and propylitic andesites; and then followed, in order, hornblendic andesites, hypersthene andesites, augite andesites, and labradorites. The last of these are evidently the precursors of the great eruptions of basalt, which began at the close of the



Pliocene and reached their maximum in the Quaternary period.

Rhyolites and trachytes, however, also occur.

The fossils of the Tertiary are very abundant, and include both marine and terrestrial forms. Among the latter may be mentioned *Hippotherium* and *Protohippus*.

#### QUATERNARY.

Quaternary deposits occupy a wide area in Mexico. They cover a large part of the central table-land, and, in a greater or less degree, the slopes of the mountains and the floors of the valleys. But, excepting the great lava-flows of the period, which are basaltic in character, they do not offer any special points of interest.

PHILIP LAKE.

## BLOOD AND THE IDENTIFICATION OF BACTERIAL SPECIES.

THE identification of any particular bacillus may be either a very easy or a very difficult matter. The detection of tubercle bacilli in sputum can be pretty safely entrusted to any conscientious medical student who has done his course of practical pathology : the determination of typhoid bacilli in the excreta of a patient may require all the resources of an experienced bacteriologist. During the last two years, however, the development and proper understanding of previous isolated or misinterpreted observations has given us a new and generally trustworthy method of recognising many species of micro-organisms. And more than this, by a simple reversal of the procedure it has been possible to supply a new means and aid to clinical diagnosis—another addition to practical medicine derived from experimental science.

So far back as 1889 Charrin and Roger (3) demonstrated that the growth of *B. pyocyaneus* (and of other bacteria) differed when made in the serum of animals immunised against *B. pyocyaneus* and when made in the serum of normal animals. The differences consisted in (i.) serum remaining more transparent, (ii.) formation of granular agglomerations and (iii.) microscopically, the formation of chains of altered bacteria, in the former mode of cultivation.

In 1891, Metschnikoff, whilst investigating *Vibrio Metschnikovi*, saw the same phenomena, and noted them as facts requiring further investigation (10). But he made no progress in this direction, being discouraged by failure to obtain the reactions with the bacillus of hog cholera.

In 1893 Issaëff made similar observations with Pneumococci, and later in conjunction with Ivanoff, with *Vibrio Ivanovi*. They attributed the effects obtained to the bactericidal and growth-hindering substances in the serum (8).



In 1895, Washbourn saw similar appearances, and remarked that the mode of growth in the serum seemed to give a good indication of its protective power (13).

All these observers appear to have worked with undiluted serum only, and that too acting for a considerable time. Although they examined the deposit with the microscope they do not appear to have investigated microscopically or otherwise, either the immediate effect of the serum on the bacilli, or the effect of diluting the serum.

In 1894 R. Pfeiffer published what is now known as Pfeiffer's reaction (11), but it was Bordet who, in 1895, trying to simplify Pfeiffer's reaction, first described any observations in which the above-mentioned neglected aspects of the question were considered. He saw the agglomeration and loss of movement, but failed to attribute any specific importance to the reaction (2*a*).

It was therefore left to Durham and Gruber, who had already been more than six weeks at work on the subject when Bordet's investigations were published, to show how valuable and characteristic this reaction could be made, and to establish its general applicability (4*a*, 6*a*).

In March, 1896, I applied the reaction to the diagnosis of enteric fever in man, but scarcity of material and other delays prevented any paper on the subject appearing before September (7*a*). Meanwhile Widal, profiting by a hint thrown out by Professor Gruber at the Wiesbaden Congress (6*c*) in April, and having more cases at his disposal, was able to publish a communication on serum-diagnosis early in July<sup>1</sup> (14*a*). Pfeiffer's reaction is observed by injecting

<sup>1</sup> Professor Widal has persistently ignored the dates given in my articles and constantly represents me as having merely confirmed his results. As a matter of fact, so far as I am concerned, the invention of serum diagnosis was made independently, possibly earlier, and arrived at from an opposite point of view. On the other hand, there are certain points, *e.g.*, (i.) action of serum from other than enterica patients, (ii.) action of human serum on bacilli other than *B. typhosus*, (iii.) variability of strength of serum in enterica patients from day to day, (iv.) difference of sera of mother and child, and (v.) desirability of accurate dilution, contained in my papers; these Professor Widal has incorporated and repeated without acknowledging their origin.

a mixture of cholera vibrios together with a small quantity of serum from an animal immunised against cholera into the peritoneal cavity of a normal animal. By withdrawing drops of fluid from the abdomen at different intervals it can be seen that the micro-organisms first lose their motility, then become transformed into spherules and finally disappear. The rapidity and completeness of the reaction depends on various factors (*e.g.*, potency of serum, extent of dilution, etc.). It is not so easily performed with typhoid bacilli.

Pfeiffer thought vital action essential, but Bordet found that the same phenomena could be observed outside the body if the temperature were kept at  $37^{\circ}\text{C}$ . He generally performed the reaction with a mixture of bacilli, "immune"<sup>1</sup> and normal serum, but he recognised that it could occur well with only "immune" serum, and also, although generally more feebly with only normal serum from various sources. Bordet laid chief stress on the granular degeneration of the micro-organisms rather than on the agglomeration into groups.

Durham and Gruber examined the phenomena much more thoroughly, and extended it to several kinds of micro-organisms. They found that the addition of a small quantity of "immune" serum to an emulsion of the corresponding bacillus in a test tube caused a precipitation of the bacilli in the form of fine granules, the supernatant liquid becoming clear. In fact the reaction resembled an ordinary chemical reaction occurring slowly. A control tube containing only bacilli would remain uniformly turbid. The rapidity and completeness of the reaction were found to depend on the same causes as in Pfeiffer's reaction. If the same experiment is performed with smaller quantities so that the process can be observed microscopically, under suitable conditions the following stages are seen. The bacilli at first isolated and moving rapidly about and across the field gradually slow down and begin to hang on one

<sup>1</sup> For the sake of brevity, "immune," "typhoid," "cholera," etc., serum will be used for the serum of an immunised animal, for the serum of an animal immunised against cholera, typhoid, etc., respectively.



to another ; groups of three or four are thus formed which then adhere to other groups, until, if the reaction be complete, all the micro-organisms are collected into large clumps, with total loss of movement. Should the serum be very potent and not sufficiently diluted, agglomeration and loss of movement may occur instantly, so that by the time the slide is brought under the microscope the reaction is already completed. On the other hand, with a weak or much diluted serum, the phenomena may remain permanently incomplete, so that several isolated micro-organisms are still seen, and even some of those in the clumps may retain their motility. So delicate, however, is the reaction that serum from a very highly immunised animal will produce an effect on its corresponding bacillus even when diluted 500,000 times. The action is to a considerable degree specific (or as Durham prefers to term it, special), for a "cholera" serum will not act on typhoid bacilli, and "typhoid" serum will not act on coli bacilli. On the other hand, "cholera" serum will affect to some extent certain vibrios which are not cholera, and "typhoid" serum will agglomerate *B. enteriditis*. But there is generally some difference, and any given serum acts best, *viz.*, in greater dilution, on its own kind of bacillus, so that it can be used for its identification, without causing confusion.

The extent to which any serum can be diluted and yet show an effect depends in part on the virulence of the culture employed ; the more attenuated the culture, the weaker the serum solution necessary to produce an effect. It is to this grouping power that Durham gave the name "clumping action" of the serum, and the hypothetical body producing it was termed by Gruber "agglutinin".

It is obvious that the reaction can be applied to the identification of various kinds of bacilli, if we possess specimens of the corresponding "immune" sera ; and perhaps, as will be indicated later, it may be of use in the discovery of new forms. In spite, therefore, of the sources of error just mentioned, a "typhoid" or "cholera" serum can prove of great use in determining whether doubtful organisms belong to these species. It is also clear that

the reverse will be true : that by means of a known bacillus we can identify an unknown serum, and can with comparative ease ascertain whether an animal is at all, or to what extent, protected.

That the "agglutinin" is distinct from the bactericidal and paralyzing substances in "immune" or other serum appears from the following considerations. An "immune" serum exhibiting strong agglutinative power need not be appreciably more bactericidal than normal serum. A normal serum may exhibit agglutinative without paralyzing action (7a). Agglutinins are not produced in the serum of animals immunised against certain micro-organisms ; *e.g.*, *B. diphtheria* and certain micrococci.

Motility of the organism is not, as was at first supposed, essential for agglomeration. Not only can agglutination occur using dead, motionless bacilli instead of active living ones (2b), but it may be seen also with some non-motile bacteria and cocci. With some cocci I have seen a phenomenon resembling the loss of movement of motile bacteria. Before the addition of the serum, the cocci usually exhibit a Brownian movement which is much restrained or even entirely inhibited by the action of suitable serum (7b).

Gruber explains the phenomenon of agglomeration by the supposition that the agglutinin causes the enclosing membranes of the bacilli to swell out and become sticky, and that they consequently adhere to each other when they come in contact. He also put forward the idea that the effect of the special agglutinin is thus to facilitate the action of the general bactericidal substances common to all sera ; and his theory of immunity is based on these two fundamental ideas.

The theory has not been unanimously accepted. Pfeiffer considers each serum to have a strictly specific action. Salimbeni does not believe agglutination to occur inside the body (12). Nobody has been able as yet to demonstrate a swelling of the capsule. Be all this as it may, the observed facts, without any theory, form a valuable addition to bacterial knowledge.

The "active" immunisation of animals is usually attained



by the injection, either hypodermically or into the peritoneal cavity, of dead or attenuated cultures of the micro-organisms. The destruction of the culture used may be effected by the use of either heat or disinfectants, but too great an application of either diminishes or destroys the immunising power of the injection (14*b*). The date on which the reaction first appears after injection is rather variable, and depends on two or three factors, although chiefly on the strength of culture. Thus a guinea-pig which I injected with living cholera culture on 18th April, 1896, showed the reaction well on the 21st, whilst one injected with dead cholera culture on 16th March, 1896, did not exhibit marked agglutinative action till 23rd March. It is not even necessary to inject the bodies of the bacteria: filtered cultures give similar but weaker or more delayed results (14*b*, 9). By the simultaneous injection of two kinds of micro-organisms agglutinins for both can be produced in the same serum (14*b*).

“Passive” immunisation is generally produced by the injection of serum from an actively immunised animal. In such a case the agglutinative property shows itself much sooner. Thus, in a guinea-pig which I injected at 3 P.M. on 9th March, 1896, agglutinin could be detected in the blood already at 3.30 P.M., and had attained its maximum strength about 6.50 P.M., remaining at the same strength for about one week afterwards. An actively immunised guinea-pig generally possesses agglutinative serum for a considerably longer period.

The nature of the agglutinating substance has not yet been distinctly ascertained. Filtration of the serum through a porcelain filter diminishes its power. Precipitation by neutral salts of the globulin of the serum or the fibrinogen of the plasma causes loss, or sometimes only diminution, of agglutinative power in the filtered fluid. Similarly serum is generally only two-thirds as powerful as plasma, so that the agglutinin seems to be in some way bound up with the proteids of the blood. Leucocytes, when shed, do not apparently give off any agglutinin. Temperature affects agglutinin in proportion to its height and the time it is

allowed to act. Ten minutes at  $75^{\circ}\text{C}$ . destroys the substance, and an hour at  $57^{\circ}\text{C}$ . causes a diminution of effect. Merely heating to  $60^{\circ}\text{C}$ . does not deprive serum of its power (1, 146).

What has been said hitherto relates nearly entirely to animals, and, of these, to guinea-pigs. We shall now consider the question mainly in relation to man.

The serum of normal guinea-pigs rarely exhibits agglutinative power, but that of some other animals, particularly of the horse, sometimes show it in a marked but varying degree. So, too, does the serum of man. The blood of many individuals possesses a pronounced agglomerating action on several forms of micro-organisms; but the quantity of each agglutinin is small, not showing itself when the serum is diluted more than eight times (7a). Thus normal human serum presents some striking differences from that of immunised guinea-pigs, principally in its multiple action. We shall consider later whether this is due to the presence of a common agglutinin or small quantities of each special agglutinin.

When normal serum has any agglomerating action it is often nearly equal on at least three kinds of bacteria—*B. typhosus*, the cholera vibrio and *B. coli communis*—and its action on each disappears at about the same degree of dilution. In one diseased condition marked by the evident presence of abnormal substances in the serum, namely jaundice, the agglutinating action is always present; and if the serum be not diluted, it is as rapid and complete as with the serum of an immunised animal. Neither normal nor icteric serum, however, possesses the power of inhibiting movement. For this reason it seems probable that during the process of immunising there are formed in the specific sera two substances, one to cause the agglomeration and another to inhibit movement, for this latter quality is nearly as characteristic of such sera as the former.

If this agglutinative property carry with it a proportionate amount of immunity then a considerable number of individuals are slightly immunised against typhoid, against cholera, and probably also against other diseases.



It cannot yet be considered settled whether this property is inherited or acquired. Experiments on animals seem to show possibility of inheritance (14 *b*), but if in these experiments the inoculations were made into the peritoneal cavity there is an obvious source of error. In the few human cases which I have been able to examine, the blood of the child was usually inactive although that of the mother was generally, sometimes even powerfully, active. In one instance where the mother had had enterica five years previously, the child's serum exhibited but very feeble agglutinative power. In one case where the child was born during an attack of enterica in the mother the serum was very active, but in another it was not so; possibly in the first case the child was also passing through an attack. If the specific agglutinins are inherited they should be found fairly frequently in the sera of new-born children, especially abroad, where a larger percentage of the population have had either enterica or cholera. According to my own observations, in Austria at any rate, a greater percentage of adult than infant sera possesses this property, tending to show that it is an acquired quality. It may be that a more extended series of observations would reverse these figures. Anyway, in light of these differences of hæmic properties, statistics on the relative immunity (if it exist) of the children of "typhoid" parents would be of interest.

It was natural to suppose, as the result of experiments on animals, that typhoid (or cholera) patients, who were thus passing through a natural immunising process, would produce agglutinins in their blood. Observation showed this supposition to be correct, and vaccination experiments on man have confirmed it. In the latter case agglutinins have been observed in the blood already on the second day after injection (15*b*). When the infection of typhoid takes place in the natural way owing to the smallness of the initial dose, the agglutinin is not generally found in the serum until two or three days after the nominal commencement of illness, *viz.*, about sixteen days after injection. This may be taken to be about the time when the contest between organism and micro-organism seriously begins. In cholera,

with its much shorter incubation period and rapid development, we should expect to, and actually do, find the reaction earlier.

If the normal agglutinin in the blood is of a non-specific character, then an attack of enterica produces an entirely new substance and does not add to what is already present, because the effect of the serum on cholera vibrios and coli bacilli remains the same, only that on typhoid bacilli is increased.

The rate of agglutinin production varies in different cases as might be expected, and there is also a remarkable variation from day to day in the agglutinative power of the serum. These variations can hardly be entirely due to experimental errors. In immunising animals I have often noticed that the agglutinative power seemed to increase irregularly. Moreover, it is known that the agglutinin is used up during its action on the bacilli, this being one reason for always employing a constant quantity of culture. Consequently, it appears possible that a rapid increase in the number of micro-organisms, which may easily occur if they light on some fresh suitable soil, would use up the available agglutinin and reduce the amount temporarily below what it had been the day before and may reduce it below the level of normal blood. And it explains why the most severe cases of typhoid may have comparatively little agglutinin in their blood.

By the aid, therefore, of a known culture of typhoid bacilli and by suitable dilution of the serum to be tested to avoid any error due to the presence of normal agglutinin, it is possible to diagnose enterica by the agglutinin contained in the patient's blood. It is obvious that the principles of serum-diagnosis apply to other diseases as well as enterica. The method has indeed been used for the diagnosis of cholera, Malta fever and glanders. In diphtheria and tubercle it has not yet been successful. It might very well be applied also to the diagnosis of pneumonia, erysipelas, appendicitis and influenza if required, since it is not necessary that the specific organism should be motile. From a case of scarlet fever I isolated a coccus which agglutinates with scarlet fever serum (76).



One general precaution must be mentioned regarding the serum-diagnosis of any disease. Although absurdly obvious, neglect of it has already led into error; namely, that it is no good applying the test if injections of "anti-toxic" serum have been made and agglutinins thus artificially introduced.

Not only may the agglutinin reaction be applied to the diagnosis of disease already present, but is also likely to be of use in the discovery of specific micro-organisms as yet unknown, *e.g.*, small-pox, typhus, measles, etc. For this purpose bacteria must be isolated from the various tissues and their reaction with the serum of patients convalescent from the disease in question ascertained. Naturally, any positive result must be controlled with other sera, and by suitable dilution of the specific serum.

There is one source of fallacy against which it is necessary to guard. Some infectious diseases, *e.g.*, scarlet fever, and small-pox in its later stages, are nearly certainly cases of mixed infection, more particularly with the organisms of sepsis. Under such conditions more than micro-organism might give a reaction with the serum, and other criteria would have to decide which is the specific one. Partly for this reason I do not consider the coccus above mentioned to be the specific organism of scarlet fever.

Without Durham and Gruber's exact and complete investigation and extension of the older isolated observations, a valuable addition to both practical bacteriology and to practical medicine would have been, if nothing else, for some time delayed. The application of the serum test to disease in man is but the natural outcome of their work. Being now part of routine diagnosis it is past the stage when the name of any individual should be attached to it, but in the history of this new departure in diagnosis their names have the first claim to be mentioned.

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- (7) GRÜNBAUM. (a) *Lancet*, ii., pp. 806, 1559, 1745, 1896. (b) *Ibid.*, i., p. 451, 1897.
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ALBERT S. GRÜNBAUM.



## THE FAUNA OF THE GREAT AFRICAN LAKES.

IT has been known for some years from the character of the shells of the Gastropods that have been brought back by travellers and missionaries from the interior of Africa that the great lakes of this continent contain animals which are quite unlike anything existing in the true lacustrine faunas from other quarters of the earth. At the same time these lakes are so remotely inland, and so greatly elevated above the surface of the sea, that all possibility seems to be precluded of animals such as deep-water gastropods and jelly-fish being either carried into them through the air or making their way up the rivers which run out of them to the sea. To determine the nature and affinities of these animals, and to account, if possible, for their presence in the great African lakes, was the object of a recent expedition which I made to the interior, the ultimate destination of which was Lake Tanganyika. I was, however, enabled while *en route*, through the exceptional facilities given to me by Sir Harry Johnston, to spend some time upon, and to become acquainted with, the physiographical characters and the faunas of both Lake Shirwa and Nyassa.

The discovery of the Tanganyika fresh-water jelly-fish by Boehm in 1886, the character of the shells of gastropods obtained by Burton and Speke, and still more those brought back by the missionary Mr. Hoare from the same lake, are all so remarkable in themselves that a considerable amount of scientific interest has been roused concerning the real nature and origin of these singular lacustrine forms.

The mere existence of a jelly fish in Tanganyika is sufficient to suggest the idea that the fauna of Tanganyika must have been at some time contaminated by incursions of these animals from the sea, and it is the merits of this theory of *marine contamination*, if I may so call it, which I wish to discuss in some detail at the present time. I wish more especially to call attention to the amount and character

of the collateral evidence which can be brought to bear upon this question from sources other than that of the morphology of the lake animals themselves. For although at first sight it might appear an easy thing, having obtained these animals, to determine their actual affinities and thereby decide once for all whether they are marine or not, the exact reverse is actually the case. The more we know about these animals the more difficult it becomes to determine what their actual affinities really are, and recently quite a number of alternative hypotheses have cropped up. Thus it is said (1) that these animals are not marine at all, that they owe their present character to the oceanic conditions operating in a great lake; (2) that they may be a common feature of African lake faunas, and therefore simply a unique character of the African lake fauna as a whole; (3) that their peculiarities are due to the latitude in the environmental conditions of the lakes themselves; (4) that they are the remains of a prehistoric *fresh water*, possibly cretaceous stock, which has survived in some of the African lakes; and so on, till the only satisfaction felt in the contemplation of these solutions is the certainty that they cannot all be true.

It is my chief object in the present article to examine first the physiographical differences of the lakes themselves, so as to be able to form some sort of an estimate of the effect these differences are likely to have produced in the faunas of the different lakes, and, secondly, the actual facts, so far as they have been at present ascertained, regarding the distribution of the families and genera of the aquatic animals among the lakes themselves.

When the evidence relating to these two lines of inquiry has been collected it will be seen that the greater number of the foregoing hypotheses are clearly incapable of application to the problems they were made to solve, and that there remains a direct issue between the respective merits of only three. Lastly it becomes apparent, when attempting to decide which of these three residual hypotheses really explains the nature and origin of these remarkable African lake forms, that the evidence drawn from the morphology of these animals themselves alone has any weight.



The larger African lakes are for the most part situated in the tropics north and south of the Equator, the bulk of Nyassa lying between  $10^{\circ}$  and  $14^{\circ}$  south. This lake is 1500 feet above the level of the sea, some 340 miles from north to south, and from twenty-five to forty miles across. Its water is profoundly deep, soundings of more than 300 fathoms, no bottom, having been obtained over a great portion of its length. The water of this lake, therefore, goes below the level of the oceans on each side of the continent, and from its immense size it acquires all the superficial characters of a stretch of sea such as the Baltic or the English Channel. The fauna of such a lake is exposed to the full force of storms and currents and to the effects of heavy surf, while owing to its altitude the superficial layers of water are at a considerably lower atmospheric pressure than those of the lakes and rivers on or about the level of the sea. Nyassa, moreover, has a broad outlet to the ocean to the east, and the water of the lake is thereby kept peculiarly sweet and fresh. These conditions are very different from those obtaining in Lake Shirwa, which stands about the same level at a short distance to the south. Here the water is nowhere more than about fourteen or fifteen feet deep, the lake is small in superficial extent, filled with reed patches which effectually prevent all surf, and, lastly, it is without an outlet, and consequently the organisms living in it have to endure a continually increasing salinity as the water year by year dries up.

Lake Bangweolo, which lies between Lake Nyassa and Tanganyika to the north-west, is a broad, shallow basin of water which is fresh and pure, but it stands at an elevation of 3000 feet, its basin being really a slight depression in the interior plateau of the continent, and owing to its greater altitude, the average temperature is far lower than that of the Nyassa Valley to the south. Except that it is deep, Lake Mwero is under the same physical conditions as Lake Bangweolo. Tanganyika is at a considerably lower level, 2700 feet, but it is so shut in by hills that the average daily temperature of the air and of the water of this lake are higher than those of Nyassa, although, as I have said, the

latter is only 1500 feet above the sea. This shut-in character of Tanganyika, and its consequent high temperature, is witnessed in a still higher degree in the valley of Lake Rukwa, whose lofty coasts rise almost perpendicularly from the water's edge from 5000 to 7000 feet. Owing to this cause the Rukwa region is extremely hot, and as the lake is without outlet the water is extremely salt. Again the Victoria Nyanza forms a vast expanse of shallow water like an enlarged edition of Bangweolo. But the characters of Tanganyika are repeated to some extent in the Albert Edward, the Albert Nyanza and Lake Rudolph to the north and east.

It is thus seen that the conditions under which the faunas of the lakes exist vary a good deal from lake to lake. The lakes themselves moreover vary considerably in the directness or the indirectness of their connections with each other and the sea. Thus Nyassa flows directly south and east to the Zambesi and the east coast, there being only one great series of rapids, at the Murchison Falls, throughout the whole of the effluent river's course. The effluents of Lakes Bangweolo, Mwero and Tanganyika, on the other hand, all flow together down the Lualabwa to the Congo and the Atlantic Ocean. This series of lakes is now, and must have been for a prolonged period of time, entirely cut off from all contamination through incursions of all but the most active marine animals coming up the rivers from the sea, for the courses of both the Lualabwa and the Congo<sup>1</sup> are intersected by formidable rapids and falls.

The effluents of the Victoria Nyanza, the Albert Edward and the Albert Nyanza go north and eventually reach the Nile, and in this way it will be seen that some of the great equatorial lakes have water communications with the seas and oceans north, east and west. The upper reaches of these rivers are, however, effectually blocked, so far as migration from without inward is concerned, by successions of falls and rapids where the rivers pass downwards from the high interior plateau, and of these several river courses, that from the west, stretching from the Lualabwa and

<sup>1</sup> See Stanley's description of this region in his *Darkest Africa*.



eventually reaching Tanganyika through the Luakuga, is, and must for a long time have been, the most impassable of the lot.

It is thus apparent that the general physiographical characters of the African lakes, the nature of the water in them, as well as the characters of the effluents which flow out of them when such exist, are in no way similar, they are on the contrary remarkably diverse, the physiographical characters of the lakes being, in fact, far more unlike each other than any one who was unacquainted with the wide climatic variations induced by altitude in the tropics would be likely to suppose. Such diversity in the environments to which the faunas of the great African lakes must have been, and are now exposed, would, I imagine, be regarded by all experienced naturalists as quite sufficient if this action was at all prolonged, to induce profound changes in the characters of the organisms which originally migrated into them; but I know of no method by which the effect produced by environmental difference can be foretold, all that can be done is to examine the faunas of the lakes themselves collectively, putting down those individual peculiarities they present, which do not appear to be produced by oceanic contamination, or some such entire difference of nature to the operation of this cause. It must however be borne in mind that the power of changed environment, to produce corresponding changes in animal organisation, is by no means unlimited, and certainly its effect in Africa is more often witnessed in the reduction of the number of genera in a lake, than in the production of new ones. Exceptional conditions appear to be adverse to fauna as a whole, and in no way productive of abundant variations. Change in their environment however is not the only factor which might, and probably has, operated in differentiating these African faunas one from another. As Darwin pointed out many years ago it is only necessary to run a fence across a cattle park to produce different breeds on either side of it, and the isolation of groups of animals to which this process is practically equivalent, has been carried to a high degree of perfection in many of the African lakes.

Carefully bearing in mind the above enumerated facts, we may now examine the actual distribution of animals amongst the African lakes so far as this distribution is at present known, attempting thereby in the first place to estimate how far the individual variations presented by the faunas of the different lakes may be due to differences of environmental condition, or to what extent they must be explained through the operation of some other cause.

The Molluscs of the individual lakes are the group which is at present by far the most widely known, and the Molluscs from different localities show specific differences, which are at once obvious to the most casual observer; in fact very little experience of the Molluscs of different lakes enables one to tell at a glance from which lake any particular species may have come. Thus the Paludinas, which abound in the most astonishing profusion in nearly all the African lake waters, whether salt or fresh, show all sorts of gradations in size, from the little variety found in the fresh water of Nyassa to the large angular species of Mwero, and lastly to the largest *Neothaumas* of Lake Tanganyika, which species increases in size from the south to the north of the same lake. What is true of the Paludinas is true of the other Molluscs. There are specific differences peculiar to each lake, but beyond this the differences between the lakes is generally apparent simply in the omission of more or fewer genera as we pass from the great lakes to the small. The larger lakes have invariably by far the greater number of different genera, not only of Molluscs, but also of fish, crustacea, sponges, and the like. Nyassa, which ranks third in actual dimensions, and which, owing to its enormous depth, probably contains more water than any other single African lake, has yielded about seventeen different genera of Molluscs, among which there are the following genera of Gastropods: *Limnea*, *Isodora*, *Physopsis*, *Planorbis*, *Ampullaria*, *Lanistes*, *Vivipera*, *Cleopatra*, *Bythinia*, and *Melania*. Except that of Tanganyika, the Molluscan fauna of Nyassa is the largest of any known African lake, and it will be seen from the above list of Gastropods that it is, so far as they are concerned, of an



entirely lacustrine character. But what is true of the Gastropods in this respect is true of the remaining orders and families. The lake contains those only which are usually found to be associated together in the fresh waters of all the other great continents. There are individual peculiarities in some of the species contained in these Nyassan genera which are quite sufficient to distinguish the Nyassan fauna from that of any of the other African lakes. But they are by no means so great as might have been expected if the diverse conditions which I have pointed out as obtaining in the different lakes have really been operating for a very prolonged period of time. Thus the character of the fauna of Nyassa is entirely that of an ordinary lacustrine series, and has undoubtedly been derived from a purely fresh water stock. There is no form known in this lake which has any marine attributes about it, and there is nothing to suggest in the least that the lake has at any time been in connection with the sea.

The fauna of Nyassa is, however, extremely important to the present inquiry in another way. The Mollusca found in this lake, together with the fish, crustacea, and so on, compose a list of genera which includes all those found in almost all the neighbouring lakes, and thus if we arrange the names of the Nyassan genera of Gastropods, for example, in a vertical column, and write the names of the principal African lakes horizontally along the top, it will be seen that the genera of Gastropods which have been found to inhabit the other lakes are those which are contained in the Nyassan list, more or fewer of them being represented as the particular case may be. Thus in Shirwa we have *Vivipera*, in Kela, *Planorbis*, and so on. In the Victoria Nyanza and the Albert Nyanza there are a larger number of these same Nyassan genera, and it will be seen at once from the table that the Nyassa list covers all those hitherto found in every African lake but one. This solitary exception—Lake Tanganyika—does, however, contain the Nyassa list in full, but above and beyond this list there are some seven or eight genera of Gastropods which, so far as is at present known, are found living nowhere else in the world.

The isolated group of Molluscs constituted by these seven or eight genera are, then, something *superadded* to the general African lake fauna, and all the members of this group seem to be strictly limited to the confines of Lake Tanganyika alone. The evidence on this last point, however, is, as will be seen from the appended table, not yet complete, but it is, I am convinced, sufficiently complete to show that this group of Tanganyika Molluscs is not represented in any of the lakes in which Molluscs have hitherto been recorded. They are certainly not present in Nyassa, Shirwa, Bangweolo, or Kela; and the members of the above group are so conspicuous and common when they do occur, that they would certainly have been recorded from the Victoria Nyanza and the other members of the northern group of lakes if they had existed there.

Gastropod Genera occurring in the African Lakes.					Nyassa.	Shirwa.	Kela.	Bangweolo.	Mwero.	Rukwa.	Tanganyika.	Victoria N.	Albert Edward.	Albert N.	Baringo.	Rudolph.
Limnea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isidora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Physophrisis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Planorbis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ampullaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lanistes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vivipara	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cleopatra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bithynia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melania	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neothauma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paramelania	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Typhobia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syrnolopsis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lythoglyphus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lymnotrochus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Undescribed Genera in Tanganyika	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
								No gastropods with shells according to Weatherly.		Not known.						
														</		

Table showing the distribution of Gastropod Genera in the principal African Lakes.

There is, then, not a shadow of evidence to support the idea that the remarkable forms of Molluscs recorded from Tanganyika are a characteristic feature of the African lake



faunas as a whole ; and this isolation of a number of Molluscan genera in Tanganyika is also shared by a number of fishes, crabs, prawns, sponges, medusæ, and several forms of protozoa, none of which are represented in any of the other lakes.

It becomes in this way gradually apparent that the fauna of Tanganyika is not only more profuse, but far more complex than that of its sister lakes. The fauna of Tanganyika is in fact naturally divisible into at least two distinct types or groups, one being made up of genera found to be widespread in all the other lakes, the characteristics of which are those of a typical fresh water stock ; the second made up of a number of animals peculiar to Tanganyika, and the *tout ensemble* of this latter group is marine.

The broad facts of the distribution of animals among the great African lakes lead then to this most remarkable result, that in the one lake having an outlet at all, which at present is the most inaccessible from without, there exists to-day a group of animals found not only in no other lake, but the members of which are not quite like any other species, either salt water or fresh.

Now, if the foregoing statements have been borne in mind it will very soon become apparent that this curious result effectually disposes of the first three hypotheses which were given on page 628 as possibly accounting for the existence of these animals in African lakes. The animals in question cannot be a common feature in African lake faunas, since they appear to be exclusively restricted to the confines of one lake. They cannot have resulted from the effects of oceanic conditions operating in a great lake, because these conditions are quite as much pronounced in Nyassa and the Victoria Nyanza as in Tanganyika, and if it is suggested that Tanganyika may be older than the other lakes, and that its fauna may thus have had time to modify there more than elsewhere, I would point out in the first place that the normal fresh-water faunas of the other lakes are quite as much modified as that of Tanganyika, and further that there is more direct geological evidence for the antiquity of Nyassa than for

that of Tanganyika.<sup>1</sup> Lastly, they cannot conceivably have originated in Tanganyika through the effect of environment, since this would have affected the whole of the fauna and not simply have superadded new genera to a list which in other respects is so strikingly similar to that found in Nyassa.

There remain then three hypotheses, two of which if they are not still actually tenable must receive some further consideration here. The first of these seeks to explain the existence of the unique group of organisms found in Tanganyika, by supposing them to be the persistent remains of an extinct fresh water fauna, and this view has been said to have a certain amount of palæontological support. Some of the original shells brought home from Tanganyika have for several years been regarded by many geologists, notably by White<sup>2</sup> and Tausch,<sup>3</sup> as being probably related to certain Cretaceous brackish or fresh-water fossils of America and Southern Europe, the so-called *Paramellantias* of Tanganyika being compared to the *Pyrguliferas* of Cretaceous times. The possibility of such a comparison has naturally led the way to the view that the enigmatical Tanganyika animals may not in reality have resulted from the marine contamination of the lake, but be the survivals of a prehistoric fresh-water stock, which once upon a time existed widespread in Africa and in Europe and America also. But although there is the most remarkable similarity between the *Paramellantias* of Tanganyika and the fossil *Pyrguliferas*, it must, I take it, be confessed that the determination of a real identity between fossil and living shells of this sort is hazardous in the extreme. For example, if the singular *Lymnotrochus* of Tanganyika had become fossilised in ancient beds, it would almost certainly have been classed along with the true *Trochi*, although in reality it is nothing of the kind. On these slender grounds, of a similarity

<sup>1</sup> I have discussed the evidence bearing upon the relative antiquity of the lakes in a paper in the *Journal of the Royal Geographical Society* now in the press.

<sup>2</sup> *Proc. of U. S. Nat. Mus.*, S. 98, Washington, 1883.

<sup>3</sup> *Sitzungsber. d. Kais. akad. d. Wissensch.*, Bd. xc., 1, p. 57.



between ancient and living fresh-water shells, the anatomical characters even of the latter not being then known, the idea has been promulgated that the whole of the isolated group in Tanganyika has had no marine origin but represents a sort of prehistoric condition of the African lake faunas in general. There are, however, to my mind several fatal objections to such a view, first and foremost among which is the total isolation of the Tanganyika group to the lake in which it now lives. If this group were really representative of the ancient African fresh-water Cretaceous stock, more or fewer of the remaining lakes would almost certainly have contained representatives of this group, and although it has been argued that change in the salinity of the water, of which there is no proof, or some other conditions not specified may have swept the old faunas out of the remaining lakes, it is to my mind in the highest degree improbable that such causes would ever have exterminated the animals in question out of all the lakes but one. Then again the gastropods are associated with jelly-fish, animals which have always been regarded as typically marine, and to argue that in the past times jelly-fish were fresh-water organisms, because certain enigmatical shells in a lake appear to correspond with fresh-water cretaceous forms, is to my mind to make a gratuitous assumption which the facts of the case do not in the least necessitate. Lastly the *Paramelania*s themselves although presenting in the characters of their shells, such a marked similarity to the *Pyrgulifera*s of the chalk, are quite as much like some of the marine jurassic *Purpura*s, and in this way the Palæontological evidence upon the subject can be made to cut both ways. Moreover, supposing the *Paramelania*s to be really the living representatives of the Cretaceous *Pyrgulifera*s as some of the latter were estuarine forms, it is quite likely that they may have been existing in or about Lake Tanganyika, if this lake *was* in connection with the sea, and have lived on in the lake along with those marine animals which were able to stand a succession of later changes.

The palæontological evidence touching the origin of the

Tanganyika fauna is then in a most complicated and uncertain condition at the present time, but it is quite likely that more light will be forthcoming in this direction later on.

There is yet one more possibility concerning the origin of these forms which it is necessary to take into account. It is quite conceivable that the prolonged isolation which these animals living in Tanganyika have undergone may have allowed them to sport into forms simulating oceanic types, and this is in itself a most attractive hypothesis, but it is again met by the same fatal objection of the complete restriction of the marine fauna to the confines of Tanganyika itself. If these organisms were the result of sporting, why have not the faunas of the other great lakes exhibited the same sportive characters; why, for example, has the fauna of Nyassa retained its original fresh-water characters although there is more geological evidence for the antiquity of the fauna of this lake than in the case of that of Lake Tanganyika.

From all this it is apparent that the alternate hypotheses to marine contamination which may be made to account for the presence of certain animal forms in Lake Tanganyika seem one after another either to break down entirely or to become so uncertain as to be of little value, except as incentives to the production of evidence the combined effect of which has been to leave the theory of marine contamination as the only road towards the solution of the problems which the African lakes present.

Thus without appealing to the facts of morphology themselves, and quite apart from the affinities which the Tanganyika group really exhibit, it seems quite impossible to account in any way except through the hypothesis of direct marine contamination for the presence of certain animals in the lake. These objections are, moreover, something more than negative; in every case they afford positive evidence against the possibility of adopting any of the alternate hypotheses detailed above. The only remaining objection which can now be raised apart from the direct morphological evidence which may bear upon the theory of marine contamination is that such a view is rendered im-



probable by the geology of the district in which Tanganyika lies. There is, however, no such objection forthcoming; what is known of the geology of this district simply shows that the lake region has been enormously elevated and depressed in by no means very ancient times, and this is in exact accordance with the facts of morphology, as we shall see.

We have then, I hope, cleared the way to a direct appreciation of the facts of morphology themselves. We have seen that a greater number of the hypotheses which have been made to account for the peculiarities of the African lake faunas are inapplicable to the questions they were intended to solve, when the facts of environment and distribution have been fully weighed, and, lastly, that there is no evidence either geological or palæontological which in any way militates against the conclusions drawn purely from a study of the morphology of these forms being any way unsound. Whatever result can be got out of the study of the pure morphology and affinities of these animals is likely to be the best explanation of their existence in Tanganyika that can be obtained.

It would, however, be premature as well as beyond the limits of this article to enter into any detailed account of the anatomy of the individual members of the unique Tanganyika group; all I shall do is to indicate the general tendency of the investigation, as far as it has been at present carried.

The incapacity which certain members of the Tanganyika fauna present, of being directly associated with any other living species, is a most remarkable fact; it shows among other things that these aberrant lake forms must have had time to remain as they were until similar forms had become elsewhere extinct, and thus these animals still living in Tanganyika must be comparatively old.

The Medusa which was first sent home by Mr. Swann and examined by Günther has never been satisfactorily associated with any living form. The deep-water gastropods which I obtained in the lake are in the same predicament, but these forms offer many structural points, which

throw a considerable light on the real nature of the fauna to which both they and the jelly-fish belong. The Typhobias of Tanganyika which might at first sight have been regarded as something of the nature of a Paludina with a highly specialised shell, appear really to combine the anatomical characters of Bythinia, Natica, Littorina, and in some respects even of Strombus, while at the same time they possess two forms of Spermatozoa, exhibiting in this respect the characters both of a Paludina and a Murex. It would appear thus that the Tanganyika gastropods are not only unlike any living species, but that they seem to combine the characters of several, and this is exactly what we should expect to be the case if the Typhobias were a comparatively ancient form. Now what is true of the Typhobias is true respecting the genera composing the deep-water Tanganyika gastropods as a whole. We have in these animals organisms which retain characters that are found only in very distinct genera and families at the present day, and the only possible inference from all this seems to be that they retain the generalised character of ancient forms.

Lastly, these members of the Tanganyika Molluscan group which I have examined appear, on the whole, to possess characters combining those of several *living marine* genera and not those of any typical *fresh-water* forms.

As is well known many of the 'fresh-water Molluscs, like so many other fresh-water organisms, retain the characters of certain extremely ancient forms, and it is obvious from this that the forerunners of the modern fresh-water Molluscs, as for example those of the Cretaceous times, would generally be less specialised than their modern derivatives and would exhibit the remains of their ancient organisation in a more marked degree. If the Tanganyika forms were the persistent representatives of such types as these we should expect that they would present more and better marked primitive features than the fresh-water animals of the present day. The fresh-water Molluscs of Tanganyika however, combine a number of the generic and family characters belonging to a variety of living Molluscs, and



thus they are probably no older than the time of the separation of the species of Molluscs from one another, which now possess their characters separately.

On the whole then, the members of the Tanganyika Molluscan group, which I have as yet examined, appear to possess characters combining those of several living marine genera, and thus the evidence as to their origin, which can be deduced from the anatomy and characters of these animals themselves, favours the view which I formed while still on the shores of the lake, namely, that these forms have survived as the representatives of an old contamination of Lake Tanganyika with the sea, and this view is, as we have seen, not negatived nor in reality, I believe, seriously controverted by any of the objections which have hitherto been raised against it.

J. E. S. MOORE.

## THE POSITION OF SPONGES IN THE ANIMAL KINGDOM: A CORRECTION.

IN my article on this subject in the last number of SCIENCE PROGRESS, I quoted Sollas as having in 1888 (*"Challenger" Reports*, vol. xxv.) proposed the term *Parazoa* for Sponges as a group of equal systematic value with the Metazoa, and considered by him as descended independently from the Choanoflagellata. It has been brought to my notice that these ideas were put forth by Sollas four years earlier than was stated by me to be the case, namely, in 1884 (*Quart. Journ. Micr. Sci.*, N.S., xxiv., p. 603 *et seq.*). I hasten therefore to make this correction, with regrets at having overlooked the earlier memoir.

E. A. MINCHIN.



## APPENDIX.

### NOTICES OF BOOKS.

*The Biological Problem of To-day.* By Dr. Oscar Hertwig. Authorised translation by P. Chalmers Mitchell, M.A., with an Introduction by the Translator and a Glossary of the technical terms. London: William Heinemann, 1896.

Dr. Hertwig is well known for his brilliant powers, both as an original investigator and as a critical exponent of the bearings of Biological research. It is hardly necessary then to say that his book will be read with keen interest by all who are attracted by the newer results of Biological speculation.

And the value of the translation is not a little enhanced by Mr. Mitchell's extremely clear Introduction, which will enable many to appreciate the points of the argument who might otherwise be discouraged by lack of familiarity with the subject treated of.

The object of the book is to explain the issues involved in the controversies raging respectively around Evolution and Epigenesis. Dr. Hertwig adopts the latter position, and he deals some very heavy blows at the foundations which underlie the doctrines of Weismann and of others who have more or less openly declared themselves as on the side of the Evolutionists or Preformationists.

One by one the author deals with the principles regarded as essential by his opponents; he discusses the consequences of the assumption of discrete material particles as associated with the existence of as many different hereditary qualities, and he points out how impossible it is to reconcile these assumptions with the facts of regeneration and of heteromorphosis without calling in the aid of an elaborate series of accessory hypotheses.

Having finished with the destructive criticisms levelled at the germplasm theory, Dr. Hertwig devotes the second part of the volume to the outlining of his own views as to the ways and means of organisation and development. To use his own words: "I start from the conception that the ovum is an organism that multiplies by division into numerous organisms like itself. I shall explain the gradual, progressive organisation of the whole organism as due to the influences upon each other of those numerous elementary organisms in each stage of the development. I cannot regard the development of any creature as a mosaic work. I hold that all the parts develop in connection with each other, the development of each part always being dependent upon the development of the whole." These statements are supported by considerations drawn from organic form, from observed correlation of development, from the modifying influence exerted by the environment,

and so on. The obvious objection, that the author does not help us in really knowing why one organism develops in this way and another in that way, is unfortunately one which we are not in a position at present to remove. In this connection Hertwig stands in sharp contrast with Weismann. The latter has formulated a theory of heredity which was intended to enable us to understand the why and wherefore of all kinds and all grades of organisation. Hertwig, on the other hand, starts with the ovum which is already endowed with the potentialities of the species, and he is content to trace the influence of the various causes which may effect or modify the course of its development to the adult organism, without saying wherein the *inherent* forces exist which primarily determine the ultimate form. But he has at least pointed out most forcibly the difficulties in the way of accepting any of the explanations as yet suggested.

*Lehrbuch der Oekologischen Pflanzengeographie, Eine Einführung in die Kenntnis der Pflanzenvereine.* Von Dr. Eugen Warming. Deutsche Ausgabe von Dr. Emil Knoblauch. Berlin: Gebrüder Borntraeger, 1896.

It has often been a subject of lamentation, in this country at any rate, that Naturalists are not so common amongst Biologists as they used to be. This is no doubt true, and it is clearly reflected in the modern type of text-book, whether Zoological or Botanical. As regards the latter science, the causes are to be sought partly in the comparative neglect into which the study of Systematic Botany has fallen. The centre of gravity has shifted, and an intimate knowledge of the minute structure, rather than of the external forms, of plants has become perhaps a little too clamorously demanded.

But signs are not lacking to indicate that the pendulum has begun to swing back again. Many of the younger botanists have already begun to perceive that study of plants as they grow is just as indispensable as is a knowledge of the structure of their vascular bundles or of their apical meristems. And on this perception it is to be hoped performance will follow. No doubt some of the disinclination to devote much attention to the systematic branch of the science has been partly due to a sort of feeling that taxonomy is rather "played out". We do not, however, by any means concede this; and certain it is that no student who desires to be in touch with the problems of the immediate future can afford to dispense with the range of knowledge which a moderate acquaintance with taxonomy alone can give.

One of the questions which in its details is gradually shaping itself more and more clearly is the important one which concerns adaptation to the environment. We know well enough that certain districts are associated with certain types of vegetation; we want further to know what it is which determines the peculiar features of these dissimilar floras. But the more closely we examine the problem



the more intricate does it appear to be. The constituents of any one flora, be it ever so characteristic, are hardly ever uniform in their fashion of adaptation. Different plants have different ways of overcoming apparently similar difficulties. What then are the factors which determine the preponderance of this and of that type of structure?

To indicate the nature of the circumstances which are thus operative, as clearly as is at present possible, forms the main purpose of Professor Warming's book. He treats first of the physical environment, the soil, climate, illumination, state of the atmosphere, and so on, in its general relation to vegetation, and then proceeds to discuss the individual characteristics exhibited by the various kinds of floras, such as marsh, marine, alpine, xerophilous, epiphytic, and the like. He points out and emphasises the difficulties of finding a ready explanation which shall embrace the constituent features of any one flora, and further indicates how the various types may actually become mingled.

His book is full of delightful details concerning the relation of different plants with their surroundings, and if the wealth of examples he quotes only serves to frighten some of his readers into a closer acquaintance with a few additional forms of life as they live and have their being, he will not have written altogether in vain. But Dr. Warming does far more than this, and we have no hesitation in saying that his book forms one of the most important and stimulating contributions to the botanical literature of recent years. He not only indicates the rational principles which must form the basis of any intelligent study of plant distribution, but his book abounds in hints as to points which are still in need of further elucidation.

A word of caution is given against the habit of generalising too hastily as to the purpose of this or of that structure. The entire form and habitus of a plant is the result of a compromise between its different parts, and it is only by a careful comparative analysis of form and structure, coupled with a due recognition of the complicated nature of the factors which together make up the environment, that any real advance is to be hoped for.

*Dictionnaire de Physiologie.* Par Charles Richet, avec le Collaboration de MM. P. Langlois et L. Lapique. Tome Premier A—B, 1<sup>er</sup> and 2<sup>e</sup> Fascicules, pp. 672, 1895. Paris: Ancienne Librairie, Germer Baillière & Cie.; Félix Alcan, Éditeur.

The advance of a science may be estimated by the growth of its literature—the method of its growth by the manner in which that literature is arranged.

In the case of every branch of knowledge it is desirable to possess, in addition to the text-books, hand-books and monographs which are essential to a proper understanding of the subject—some storehouse in which may be found a summarised account of all that is known upon any particular point. It is, moreover, desirable that in such a store-

house the contents be arranged so as to be readily accessible to any inquirer.

Perhaps the most convenient arrangement for such a general collection is that afforded by a series of articles alphabetically arranged, by, in fact, a dictionary of the science under consideration. That such an arrangement has been a favourite one may be gathered from a glance at some of the more important branches of natural science. Thus we have dictionaries of Chemistry, of Botany, of Electricity, and others, whilst there have lately appeared several important treatises on Medicine in which a similar arrangement has been followed.

For such an arrangement to be satisfactory, however, several things are necessary. In the first place the special branch of knowledge concerned must have been in existence, and separated from its sister sciences, for a length of time sufficient to provide an array of well-established facts large enough to justify the selection of an ambitious mode of treatment; and in the second place each article must be written by a specialist in that particular branch in order that a thorough treatment may be ensured. At the same time the opinions held by the writer must not be put too prominently forward.

Up to a few years ago various causes had contributed to render undesirable any attempt so to group the main facts of physiology. Chief amongst such causes may be mentioned the youth of the science as distinct from Anatomy, Chemistry, Histology and Medicine, and the small advance that had been made in several important branches. At the present time, however, most of these objections have disappeared, and the science of physiology has made such rapid advances and become so separated off from its sister sciences, whilst at the same time the mass of facts has become so vast, that some tabular arrangement seems almost a necessity.

It is, therefore, with great pleasure that we welcome the first part of the present work. A Dictionary of Physiology, by Charles Richet, assisted by MM. P. Langlois and L. Lapicque, together with a large number of other prominent physiologists, ought to, and, judging from the sample before us, we have every confidence that it will, furnish such a complete statement of the main facts of physiology as will materially aid the future development of the science.

At present we have only the first two parts of the first volume before us, and as the whole work is to consist of five volumes this is but a small instalment. Nevertheless we have here articles from which we are able to form a fair idea of the character and scope of the whole work. Thus we have an article of thirty-seven pages on Accommodation by Wertheimer, which gives a good account of what is known on the subject. Commencing with a succinct definition of the subject and proofs of its importance, the author proceeds to set forth the opinions which have been held as to the mechanism of accommodation.

The *rôle* of the crystalline lens and the cause of its change of form is described at length, and tables are given of the data of dioptric



measurements obtained by various observers (Helmholtz, Knapp, and others). The amplitude of accommodation and the rapidity with which it is effected are treated somewhat fully, and the author concludes with a description of the mechanism of accommodation through the animal series (mammals, birds, reptiles, fishes, batrachians and invertebrata).

Acromegaly is treated by Paul Blocq, Actinomycosis by F. Heim, Visual Acuity by Nuel, and Addison's Disease by P. Langlois. From this it will be obvious that the work will be of interest not to physiologists alone, but also to physicians and medical men generally. Of the advantage of physiological facts being brought to the notice of the medical profession there can be no doubt when we have before us such an instance as the recent advance in the treatment of myxœdema by the extract of thyroid gland. It is to be expected that similar results will follow the application of scientific experiments in the case of diseases at present regarded as but little amenable to treatment.

A valuable article on the Albuminoids by J. E. Abelous extends to thirty pages, and a copious bibliography is added.

Gabriel Pouchet writes an article of seventeen pages on Alkaloids, whilst more than thirty pages are devoted by Heim to the physiology of the algæ.

A very interesting article on Aliments, extending to nearly a hundred pages, is contributed by L. Lapique and Charles Richet, whilst a short but useful paper on Aluminium is written by A. Chassevant.

One of the most important papers in the portion of the work before us is the very able historical and critical essay on Anæsthesia and Anæsthetics, by Charles Richet, in which after a historical introduction we find a discussion on general and local anæsthesia and the various agents which have been used for producing these. We are in agreement with the author in most of his statements. We note that he supports the conclusions arrived at by the Hyderabad Chloroform Commission, and believes that the heart almost invariably continues to beat—and the patient is therefore recoverable, provided proper means be adopted—for some minutes after natural respiration has ceased. We note also with satisfaction that he emphasises the facts established by Paul Bert and his pupils of the importance of administering the anæsthetic in feeble, progressive doses, rather than in strong doses without admixture with sufficient air. With his criticism of the various agents employed, however, especially with his statement that mixed anæsthetics have been given up, we are unable to agree, for the A.C.E. mixture is still largely used in some London hospitals. After all, however, this is a matter of custom more than anything else, for whilst at Edinburgh chloroform is almost always the agent selected, in London ether is far more frequently used. Some of the other articles contained in the first two parts of the first volume are:—

Antisepsis and Asepsis,	-	By E. Trouessart.
Antitoxins,	- - - -	„ Charrin.
Aphasia,	- - - -	„ E. Lahousse.
Arachnids,	- - - -	„ F. Plateau.

The short paper on Anthropology by Louis Lapicque shows how little has at present been accomplished in the way of a comparative study of the physiology of different races of men.

The book as a whole strikes us as likely to be useful, and provided the rest of the articles are up to the standard of those at present published, physiologists will be provided with a reliable and conveniently arranged statement of the more important facts of their science as it exists to-day.



## APPENDIX.

### NOTICES OF BOOKS.

*The Diseases of Children's Teeth.* By R. Denison Pedley, M.R.C.S., L.D.S. Eng., F.R.C.S. Edin. London: J. P. Segg & Co.

When the medical student, having successfully passed his last examination, settles down in the country to the practice of his calling there are many things which he finds he is imperfectly acquainted with. Even the industrious ones who have conscientiously devoted their attention to the lecturer's words and have read steadily for many months begin to realise at last that medicine is an immense subject, which it takes many years to master.

More especially is the deficiency felt in the case of those subjects dealt with in the Special Departments, both because these are considered of minor importance by many and also because in some hospitals the opportunities of work afforded by these Departments are few.

But however the deficiency of knowledge comes about, it is equally deplorable, and the newly fledged practitioner can only turn for help to his perhaps scantily furnished library. Woe to him if his choice of books has not been wisely made! Books bearing upon the special diseases of throat, ear, skin and eye will probably be conspicuous by their absence; and indeed it is scarcely desirable that the general practitioner should undertake any but the most trivial operations in connection with these, always supposing that he is within reach of a good hospital.

In the case of the teeth, however, it is different. With a comparatively small amount of knowledge, much can be done to preserve—at any rate for a time—teeth which without attention would infallibly be lost. Of still more importance is it that proper attention should be devoted to the teeth of children, in whose case lack of proper care may, and very probably will, result not merely in deformity of the mouth, more or less serious, but also in the premature loss of members of the permanent dentition.

A book in which the student and the young practitioner can find set before them in a simple and yet thorough manner the more important points to be attended to in the care of the teeth, and the

best means of dealing with mischief which has already occurred should such necessity arise, will be valuable in proportion as its explanations are lucid and its directions easily followed. In the book given us by Mr. Denison Pedley we have a perfectly clear explanation of the changes mostly to be feared in the teeth of children (and to a great extent in the teeth of adults also), together with instructions as to the best means to be taken in order to avoid subsequent mischief to the permanent dentition.

That such attention to children's teeth is desirable is plainly indicated by the figures given in the chapter on Oral Hygiene, where we learn that of 3800 children examined there were only 828 in which neither filling nor extraction was required. Of temporary teeth there were, in 1460 children, 3187 which could have been saved by proper attention, whilst the number requiring extraction was 2491. There were 3511 permanent teeth which required filling, and 1506 were so carious as to require extraction.

The children examined belonged to the poorer classes, and the boys are either taught a trade or enter the army or navy. The girls are trained for domestic service.

During 1890, 55,673 recruits were examined and 21,712 were considered unfit for service. Of these, 506 were rejected on account of the "loss and decay of many teeth".

The troubles of a domestic servant suffering from neglected teeth need little imagination to picture. Besides the pain of the decaying teeth themselves, we have to consider the troubles of the digestive and other systems, consequent upon the presence of carious teeth in the mouth.

We are glad to notice that Mr. Pedley continually draws attention to the effects of carious teeth on the nervous and other systems, as we have long been of opinion that much of the pain complained of by patients is due to defective teeth. Indeed, the improvement produced in the general health by the removal of the diseased structures is often very great, and this may even be the case when no pain in the mouth has been experienced.

Of the advantage likely to be gained by the removal of carious teeth in the case of children suffering from chorea, the following is a good example:—

H. B., aged eight years. Chorea of seven weeks' standing. She did not improve at all during the first two weeks in the hospital. A painful stump was removed. In four days all movements ceased and did not recur.

This is only one of numerous examples given.

Mr. Pedley also gives examples showing the good resulting from a similar procedure in cases of diarrhœa caused apparently by the reflex nervous irritation of decayed teeth, and attempts to show that other diseases due to the absorption of septic material may be caused by infection taking place through carious teeth.



We see no reason to suppose that such infection is in any way impossible.

In the chapter on Treatment the main points to be observed and the best means of dealing with the more common forms of disease are set forth with admirable clearness. The instructions given are sufficiently full to enable the practitioner always to relieve pain and in almost all cases to do sufficient in the way of stopping the decayed teeth to ensure their preservation until such time as a dental surgeon can be consulted. Stress is laid upon the importance of recognising the first permanent molar from its neighbouring temporary teeth, as, whilst the latter have only to serve their purpose till about the twelfth year, the former has to last the child through life.

In the matter of extraction of teeth, directions are given for the effectual removal of the various teeth from the upper and lower jaw, and those cases are indicated in which this drastic treatment is absolutely necessary.

The book ends with a short article on Tartar and its removal.

We wish cordially to recommend this work of 260 pages, not merely on account of the clear and concise manner in which it is written, but also because of the immense importance to the comfort and well-being of the community of the matters of which it treats. Indeed, we regard it as a book which no general practitioner can afford to be without.

*A New Course of Experimental Chemistry.* By John Castell-Evens, F.I.C. Thomas Murby. Price 2s. 6d.

This book consists of three parts. Part I. (pp. 1 to 96) is a mixture of arithmetical problems and elementary chemical experiments, the experimental work only occupying thirty-three pages. So curiously is this mixture compounded, that on casually turning over the pages one might almost fancy that by mistake a few stray leaves of some elementary practical chemistry had got accidentally bound up among the sheets of a book of arithmetical problems. There appears to be little connection between the experiments and the problems; thus, pages 17 to 24 contain physical problems on specific gravity, specific heat, latent heat, heat and work. These eight pages are followed by three pages of practical matter, consisting of a few experiments designed to show the composition and properties of water. Then come eight more pages of physical problems, including exercises on the dynamical theory of gases, in the middle of which there is sandwiched a single page containing four more experiments on water.

Of the problems themselves little need be said; most of these will be useful exercises for the student. Some, however, are a little ambiguous; *e.g.*: "Four grains of iridium at  $1400^{\circ}$  C. are put into 100 grains of mercury at  $10^{\circ}$ ; what will be the result?" (p. 64).

Others require correction; thus on page 9: "Give on the three scales the absolute temperature corresponding to the following 'critical temperatures' of various vapours and gases". Of the eight gases named, the critical temperatures of six are incorrectly stated. Although this fact is of no consequence from a purely arithmetical point of view, it is obviously desirable from other considerations that the temperatures given should be the true ones.

The directions which the author gives for carrying out the various experiments suffer very much from over-condensation; thus, a student to whom it is necessary to say "cut a piece of clean *solid* phosphorus" (p. 11), or "fill six small cylinders with the evolved gas over *clear tap* water" (p. 38) (the italics are ours), would be at some loss to know how to set about the following experiment: "Put about 10 grains of fairly finely divided copper in a hard-glass tube, weigh it, and having raised it to a fair red heat pass about 5 litres of air repeatedly over it. When no further change occurs in the volume of the air stop the experiment and allow the tube to cool, then weigh it" (p. 13).

The book contains no illustrations, nevertheless we find such directions as the following: "Through the tube A B (App. 76, *a*) pass a current . . . close the taps E and F, and into the limb B pour some mercury," etc., etc. (p. 61). One seeks in vain for any explanation, but what "App. 76, *a*" refers to does not transpire.

The arrangement of the subject matter is somewhat lacking in method; thus, the section headed "Studies on Combustion" is made to include the following:—

Preparation of sulphur dioxide from copper and sulphuric acid.

Conversion of sulphurous into sulphuric acid by nitric acid.

Formation of sulphur trioxide.

Experiment to illustrate the manufacture of oil of vitriol.

Preparation of nitric acid from nitre and oil of vitriol.

Preparation of ammonia from ammonium chloride and lime.

Misleading definitions of *acids* and *alkalis*.

Experiments on neutralisation.

Experiments showing heat evolved on the solution of certain substances in water.

Part II. (about 120 pages) is called "Introduction to Chemical Analysis". In it the author attempts to teach qualitative and quantitative analysis simultaneously. Without discussing the doubtful wisdom of this plan, it may be enough to point out that by the time a student has reached the stage of testing for sodium, potassium, and ammonium compounds, he will, if he has followed the course laid down in the book, have made some hundreds of quantitative estimations. The sections devoted to groups I. and II.*a* (silver, lead, mercury, bismuth, copper, and cadmium) include alone upwards of fifty quantitative determinations. Indeed, the author seems to have tried to squeeze the whole science of chemical analysis into the compass of his little book; thus, in the five and a half pages given to the reactions of the negative (acid)



radicals of group I., quantitative estimations of the following out-of-the-way elements are included—*tungsten*, *vanadium*, *selenium*, *tellurium*, *molybdenum*, *titanium*, and *uranium*. The condensation necessary in order to pack so much matter into so little space, reduces the descriptions of methods to the most sketchy outlines, and the student would find it impossible to carry out the experiments without constantly applying elsewhere for instruction. This, however, is apparently what the author aims at, for at the beginning of Part III. (a useful Appendix, containing brief directions for making certain inorganic preparations), he says: "Let it ever be borne in mind that the great object of every experiment is not the mere attaining of the actual result of such experiment, but to give the student opportunities for reasoning and thinking, and the teacher opportunities for helping". A class of students working through this book would most unquestionably afford their teacher ample opportunity for helping; whether the other desirable end would be accomplished is not quite so certain.

*Kirke's Hand-book of Physiology.* By W. D. Halliburton, M.D., F.R.S. Fourteenth Edition. London: John Murray, Albemarle Street, 1896.

No better means could be adopted of gathering a general idea of the progress and evolution of Physiology, not only as taught in our medical schools but generally as a Science, than to arrange in chronological order the fourteen editions which have done honour to the name of Kirke. Perhaps the most striking evidence that could be derived from such a comparative examination would be the gradual emancipation of Physiology from the influence of pure anatomy and surgery. In the days of the early editions of Kirke it was the anatomists and surgeons who taught Physiology, and it was anatomists and surgeons who edited Kirke, as witness the names of James Paget, William Savory, and Marrant Baker, all of whom were associated in turn with the editorship, and all of whom were distinguished Fellows of the College of Surgeons. Professor Halliburton, the present editor, is the first, in a long series, who is in no way associated with the teaching or practice of surgery, moreover he is a fellow of the sister college, namely, the College of Physicians, a Physiologist of European reputation and a Fellow of the Royal Society. The present edition severs the long historical association between Kirke's Physiology and St. Bartholomew's Hospital. For fifty years this great hand-book has been edited from the latter school of medicine; and by a strange irony of fate almost the very day that gave birth to the new edition also witnessed the death of Marrant Baker, who had for so many years been intimately connected with its destinies. The new edition is entirely re-written, and, excepting in external appearance, bears little resemblance to its precursors. The previous editions had all followed closely on the lines of the ones that immediately preceded them, and in this connection it is interesting to note

that Marrant Baker in his first preface remarked that in editing Kirke only two courses were open: either to entirely re-write the work, or else to follow closely on the lines of the original author, adding such matter as the progress in Physiology made imperative. Marrant Baker adopted the latter course throughout his seven editions. Dr. Halliburton has accepted the other alternative; and the magnificent text-book which he has elaborated proves that his decision was a wise one, and that his confidence in himself was fully justifiable. Although Professor Halliburton is perhaps best known as an investigator of the chemical side of Physiology, it is impossible to detect in the new edition any undue preponderance of matter dealing with this side of the Science; indeed, if one were to pick out any one section as being better than the others, it would perhaps be that which treats of the structure and functions of the nervous system. In this, all the latest work of Ramon y Cajal, Mott, Golgi, Gowers, and many others, is ably summarised, without being overburdened with excess of technical detail, and a most valuable addition is a projective scheme of the cells and fibres of the brain, spinal cord, and peripheral end organs, constructed for the work by the author, with the assistance of Dr. Mott. This scheme presents most adequately the state of our present knowledge on the subject, and is founded on sound physiological data, and contrasts strikingly with many of the hypothetical schemata of a few years ago. Another valuable addition is that excellent diagram of Ramon y Cajal of the expansion of the auditory nerve in the cochlea. Altogether, there are something like 100 more illustrations in this edition than in the one that preceded it, and many of them greatly enhance the value of the hand-book from the teacher's as well as the student's point of view. As for the text, where all is excellent, it is unnecessary to particularise, and it is not too much to say, that if "Kirke" has lost anything in the abandonment of old tradition, it will certainly gain in prestige in that wider sphere of physiological thought and teaching over which Professor Halliburton exercises an undoubted influence.

*A Popular Exposition of New Zoology.* By K. Mitsukuri. Tōkyō: 1895.

Under the above title Professor Mitsukuri of the Imperial University of Tōkyō, Japan, has lately issued a popular work dealing with the broad principles of the study of animal life. The book is fully illustrated by woodcuts, which are simple and well chosen. After an Introduction, in which a well-selected list of General Treatises is given, there follow seven chapters dealing in order with "The Natural World," "The World of the Living," "The Number of Living Things," "The Kinds of Animals" (three chapters) and "The Fundamental Principles of Classification". These are succeeded by seven other chapters, devoted in succession to the Anatomy, Histology, Reproduction, Development, Growth, Distribution, and Colours of Animals; and the whole is



summed up in a "Conclusions" chapter, which is followed by a couple of Appendices, in which some good advice is given to teachers and those who would pursue the study of Natural History alone. Despite the rapidity of scientific advancement and assimilation of Western ideas in the far East, the study of Zoology is still largely regarded as a more or less harmless pursuit, interesting it may be, but unworthy the serious attention of the intellectual man. Professor Mitsukuri's book is in reality a plea for the Science of Zoology. It is charmingly written and, for an elementary treatise in an Eastern tongue, remarkably free from dogmatism. It has been the outcome of a dozen years' careful compilation and forethought, and is in every way worthy the important work which its author and his fellow zoologists have accomplished, by which none have more greatly benefited than we at home.

*Mechanics.* By Linnæus Cumming, M.A. London: Rivington, Percival & Co., 1896. 247 and viii. pp. Price 3s.

This is a small elementary text-book designed for the use of school-boys, and embodies the results of the author's experience in teaching a class in experimental mechanics at Rugby School. The order in which the subjects are treated is Statics, Dynamics, and Hydrostatics. Although there is no doubt that to the average beginner statics is much easier than dynamics, there are many objections to the order adopted by the author. Not the least of these lies in the fact that all through the statics the forces are measured in pounds. When, however, dynamics is reached a new unit of force, the poundal, is introduced, and suddenly what has up to now been called a force of  $x$  pounds is called a force of  $x$  pounds weight. The author in this connection does not explain how in the gravitational system the fundamental units are those of length, mass, and *force*, and that the unit of mass in this system is really  $g$  lbs. There are one or two slips we have come across; thus on page 138 it is stated that every physical quantity can be expressed in terms of the units of length, mass, and time, when it is now generally considered that temperature, specific inductive capacity and permeability form subsidiary fundamental units, at any rate in the present state of our knowledge. Again, a water-wheel is said always to work by the abstraction of the kinetic energy of the water, while in England the "overshot" wheel is quite common. The style of the book is on the whole clear, and the experimental illustrations easy of performance and carefully described, so that the work will probably be found useful for teaching beginners.

*An Introduction to Structural Botany.* Part II.—*Flowerless Plants.*  
By Dukinfield Henry Scott, M.A., F.R.S., etc. London: Adam & Charles Black, 1896.

It is with much pleasure that we welcome the appearance of the second part of Dr. Scott's *Structural Botany*. The author deals with

the Cryptogams in this volume, and it forms indeed an admirable introduction to a study of these plants.

The treatment adopted is methodical, and the essential points of contrast and comparison between the different groups are well brought out. It is satisfactory to notice that that highly specialised form, *Marchantia*, which has usually had to do duty as the representative of the Hepaticæ has here given way to a more generalised type as seen in *Pellia*. We cannot, however, suppress a feeling of regret that space did not admit of a little more recognition being accorded to the foliose of Liverworts. Not only are they exceedingly numerous as regards species, but they are also very rich in interesting forms.

The Algæ and Fungi strike us as being very well done, and we are glad to see that *Ulothrix* occupies the prominent position to which its own intrinsic importance and the ease with which it can be obtained justly entitle it.

The clear summaries and the numerous illustrations increase the value of one of the very best elementary text-books of Botany which have appeared for many a year.

*Worms, Rotifers and Polyzoa.* Being Vol. II. of the Cambridge Natural History. Edited by S. F. Harmer, M.A., and A. E. Shipley, M.A. "Flatworms and Mesozoa," by F. W. Gamble, M.Sc. "Nemertines," by Miss L. Sheldon. "Thread Worms and Sagitta," by A. E. Shipley, M.A. "Rotifers," by Professor Marcus Hartog, M.A. "Polychæt Worms," by W. B. Benham, D.Sc., Hon. M.A. Oxon. "Earthworms and Leeches," by F. E. Beddard, M.A., F.R.S. "Gephyrea and Phoronis," by A. E. Shipley, M.A. "Polyzoa," by S. F. Harmer, M.A. London: Macmillan & Co., Limited, 1896.

The death knell of the "Class Vermes" has long been rung, and under orderly arrangement, consequent on extended and detailed investigation, the vast accumulation of animals which in the last generation were relegated to that assemblage have been resolved into a series of well-defined groups which form the subject matter of the greater portion of this volume. In effecting this re-arrangement none have been more active in our own country than Messrs. Beddard, Benham, Gamble, Harmer, and Shipley—each a foremost worker in his own department; and when it became known that these gentlemen were to co operate with Miss Sheldon, a recognised investigator of allied forms of life, and with Professor Hartog, in the authorship of the volume now before the world, expectation ran high, in the hope of a work which would do credit to English zoologists, and would be found to contain something beyond the hum-drum colourless take-all-and-do-as-you-like-with-it recapitulation of ill-assorted details, familiar in a certain class of continental text-books. It was to be expected that that judicious selection of facts which is the highest function of a scientific author would be brought



into play. The time has passed at which one writer can be expected to produce unaided a well-balanced handbook on all branches of Zoology, and the co-operation of a number of authors for the production of the present treatise alone gives it a claim upon our attention.

Let it be said at once that as concerning the "Vermes" our fullest anticipations have been realised, that the chapters on Rotifera by Professor M. Hartog and on Polyzoa by Mr. Harmer are equal in merit to the rest, and that the whole volume is a worthy successor to its immediate predecessor on the *Insecta*—than which no better text-book exists in the English language.

The volume opens with a scheme of the classification adopted, carefully arranged in tabular form with full-page references to the text, and then follows Mr. Gamble's section on the Platyhelminthes and Mesozoa. The ninety-six pages of this teem with interest and contain many very new and careful observations; and not the least noteworthy feature of it is the introduction of new figures of rare merit. Figures such as Nos. 5 and 17 both in execution and design are of an entirely new order, and they reflect the highest credit on author, publisher, and all concerned. The inclusion of Frenzel's *Salinella* and Schulze's *Trichoplax* among the Mesozoa is perhaps premature, and it were better to have dealt separately with such forms pending confirmation and fuller investigation.

The Nemertinea, Nemathelminthes, and Chætognatha, are treated in a thoroughly sound elementary manner, although we could have wished for more illustrations of the former.

It is on turning to the Rotifera, Chætopoda, and Hirudinea, that we meet with the greatest novelties and newest treatment. For the first time in his own language, the English student is placed in possession of an adequate account of the structural limitations of the Oligochæta, Hirudinea, and Rotifera, free of cumbersome detail and embodying those salient facts of structural similarity and dissimilarity upon which alone the inter-relationships of the groups and their position in the scale of animal life can be at all adequately determined. More especially be it noted that the existence among Oligochætes of female gonads and ducts in a state of organic continuity, and of male pores in front of female, that the development and metamorphosis of the cœlom among the Hirudinea, together with other features which unite those animals to the Chætopoda and necessitate the rejection of the time-honoured idea that Leeches arose directly from Platyhelminthes, are luminously set forth by Mr. Beddard. And he gives the student an up-to-date insight into facts of structure and development which in course of prolonged observation have led him and others to the conclusion fast gaining ground that the metamerically recurrent type of nephridium is the more primitive, and that between the diffuse excretory apparatus of certain Chætopoda and Hirudinea and the Platyhelminthes there may be no close relationship—the latter being perhaps a system *sui generis*, in which the tubes seek out the primary centres of destructive

metabolism, much as do the tracheæ of Insects. More might perhaps have been said concerning the limits of modification and development of the chætiparous system, and it is not a little remarkable that Mr. Beddard should have omitted reference to the larval sensory apparatus of *Acanthodrilus* which he himself discovered.

Dr. Benham's chapter opens with a sufficiently detailed and guarded account of *Dinophilus*, *Polygordins*, and *Pontodrilus*, classified together as the Archiannelida. He then passes on to the Polychæta, and gives us a succinct account of their structure, development, and life history, with ample allusion to habits—especially as related to peculiar morphological adaptations. We note with much satisfaction the incorporation of the very careful and praiseworthy observations of Watson upon tube-formation, of the like of which we cannot have too many in these days of reckless generalisation upon wholly morphological characters. Asexual reproduction is adequately treated, the wonderful *Syllis ramosa* and *Eunice tibiana* find appropriate places in the text, and, as with other sections of the work, coloration, luminosity, and regeneration, are in due course considered. Distribution and palæontology come in for due notice, not altogether with the novelty which characterises the work of other contributors to the volume, however, for the paragraph on the "palæontology" of the Nemertines is worthy that so notorious on Snakes in Iceland. Better and more numerous illustrations appear to us desirable for this portion of the work, especially as delineating the "Trochosphere" larva. That given (fig. 145) is exceedingly poor, and even the familiar "Lovén's larva" series of earlier text-book writers would be welcome.

Concerning phosphorescence, we are pleased to note that the author of the chapter on the Oligochæta omits all reference to the paper by Secchi, cited in his "Monograph of the order Oligochæta" to which he frequently alludes, for it in no way deals with Earth-worms.

For the two concluding chapters by the Editors we have nought but praise. Their well-known researches during the last decade upon groups of animals dealt with in this volume led us to anticipate success, and they have not disappointed us. Novelties like the discovery of the Nemathelminthes Arhynchidæ, and careful observations like those upon the processes of budding and reproduction among the Polyzoa, are now seen to have been related to a laborious piece of work on the student's behalf, for which it is difficult to adequately return thanks. We are especially grateful to Mr. Harmer, whose pages of the book are a fitting corollary of his well-known monographs, which have always appeared to us of equally high literary and scientific merit.

Mr. Harmer deals by preference with the British Polyzoa, and gives a valuable key to their identification; but we do not consider this sufficient justification for omission of all mention of the arenaceous Polyzoon *Cryptozoon* discovered by Bracebridge Wilson and described by Dendy from the Australian seas, and of genera so remarkable as



*Kinekoskias* and *Ascorhiza*. We could have wished also a fuller treatment of the lophophore and epistoma, especially as concerning their probable non-homology throughout the Brachiopoda and Polyzoa, and at least a mention of spicule formation.

The use of the "etc." is in a scientific work indefensible. The term "trochosphere" might have been advantageously replaced by "trochophore" throughout, and mention might have been made of the important observations of Goto upon *Diplozoon*, and of Hill upon the development of the cysticeroid in *Polycercus* and *Monocercus*, and of the scolex in *Synbothrium*. We note with pleasure the recognition of Goto's masterly monograph upon the Trematoda monogenea of Japan—foremost among the productions of the East in systematic Zoology, and could have wished full reference to Martin Woodward's observations upon the numerical variation of the ovaries in the common Earthworm. Wilson's alleged discovery of the opening of the head-kidney of the larval *Hydroides* into the proctodæum should have been recorded, together with a number of other discoveries by contemporary investigators, recapitulation of which is in these pages impossible.

Zoology, like most things, is now suffering from the effects of the scramble of life which has overtaken all men; and it is interesting, though accordingly not surprising, to note that during the publication of this work the mysterious *Trochosphæra* has turned up in the Havana river, that living Land Nemertines have been found in New Zealand, and that Tower has unravelled the detailed structure of the Cestode nervous system. And we find ourselves unable to decide whether the recent discovery of the entoparasitic *Myzostoma artemia* was or was not announced in time for incorporation in the volume. Burger's revolutionary classification of the Nemertines has just come in time for incorporation, and we hail with delight that of Kowalevsky's work on the wonderful germs *Acanthobdella*.

There are many parts of the book which might be extended, but it must first be tried in its present form. *Phoronis* is rightly placed approximate to the Polyzoa, but *Cephalodiscus* and *Rhabdopleura* stand over for treatment with *Balanoglossus* and the vertebrata. We could have wished it otherwise, and we await with interest in this connection the volumes on the Echinodermata and Chordata. Professor Hartog rejects the time-honoured comparison of the Rotifera with the Trochophore, with its familiar refrain, in preference for a Pilidium larva association, which seems to us even less justified. The biporal stage in the development of *Amphioxus* suggestive of the remarkable *Salinella* appears to be passed through by some Echinoderms; all the more reason therefore that the Mesozoa should have been dealt with independently. Indeed, with regard to the inter-relationships between the present volume and its predecessors, we would have preferred the treatment of the Polyzoa, Brachiopoda, Rotifera, and Gephyrea, with *Phoronis*, in one volume, and the reservation of independent volumes for the rest of the "Vermes" and the Mollusca.

Original illustrations such as figs. 5 and 17 and copies such as figs. 12, 18 and 234, are not to be beaten; but we would have more of them. Paper and printing leave nothing to be desired; and, as for style, the portions of the work dealing with the life-history of the Tematoda and the fissiparous process in the Polychæta read like a romance. The Editors have this time kept their forces well in hand, and with co-authors and publishers have executed their work in a manner worthy a new departure by a great nation.



## APPENDIX.

### NOTICES OF BOOKS.

*Alternating Currents and Alternating Current Machinery.* By Dugald C. Jackson and John Price Jackson. Pp. xvii and 729. New York: The Macmillan Co., 1896.

This is the second volume of a text-book on electromagnetism and the construction of dynamos, and deals, as the title shows, with alternating currents and alternating current dynamos and motors. Unlike many books on kindred subjects that have been published it is neither a catalogue of commercial machines with the figures taken from makers lists, nor is it a text-book on pure mathematics with nothing but its title to connect it with actual practice. In the fourth chapter which deals with graphical and analytical methods of solving problems in alternating current circuits the authors have, perhaps, allowed the mathematical part of the subject too much play and have gone into cases which are hardly likely to ever occur in practice. On the whole, however, we strongly recommend the book to the attention of those who, being engaged in practical electricity, are not frightened because on opening a book they see the integration sign.

*The Elements of Physics.* By Edward L. Nichols and William S. Franklin. Vol. ii. Electricity and Magnetism, pp. 261. New York: The Macmillan Co., 1896.

This volume forms the second of a complete course on Physics intended as a college text-book. Although there are 227 cuts in the 261 pages and the type is large the authors attempt to touch upon most of the points in Electricity and Magnetism. The result is that as a note-book for refreshing the memory the work is excellent, but we sincerely pity the student who attempts to tackle the pages without having previously acquired a fairly extensive knowledge of these subjects. A very serious objection to the book from the student's point of view is that the references are most of them to § 000. This careless omission occurs again and again not only when the cross reference is to the third volume, but even when it is to another part of the volume under notice, and also when referring to original papers in Scientific Journals the page is given as 000.

*How to Study Wild Flowers.* By the Rev. George Henslow, M.A., F.L.S., etc. With 57 Illustrations. Religious Tract Society. 1896.

The writer of this little volume desires to impress on the teachers of Botany in schools the necessity of accuracy on the part of the pupils.

Admirable advice; but why did the author himself refrain from setting the first example? We do not mean to imply that the book is entirely a bad one, far from it; some good points it undoubtedly possesses, and it may even prove useful. But does Mr. Henslow really think that gymnosperms, as illustrated by Coniferæ, are to be regarded as Dicotyledons? And why does he confound Endosperm with the very different body Perisperm? These examples by no means exhaust the errors which a glance through the pages of his book has sufficed to discover; but the mention of them is enough to prove that, although the general line adopted may be reasonably commended, anybody who relies exclusively on its author's guidance (in spite of his "experience as an examiner for the past forty years") will subsequently find out that he will have some things to unlearn.

*Essays.* By George John Romanes, M.A., LL.D., F.R.S., etc. Edited by C. Ll. Morgan. London, New York and Bombay: Longmans, Green and Co., 1897.

Many people will welcome this volume of essays by the late Mr. Romanes which Mr. Lloyd Morgan has collected from various reviews and periodicals.

The essays themselves hardly perhaps demand criticism; they were written originally as contributions to current literature, and some of them date as far as sixteen years back. But they possess more than the mere ephemeral importance which often attaches to magazine articles; each one of them is a serious and honest attempt to deal philosophically with questions which not only interested people in the past but which still continue to attract the attention of educated persons. And it is no small tribute to their intrinsic excellence to be able to say that they still retain in a remarkable degree a decided freshness and appropriateness to present conditions of thought.

In brief the collection is one which not only the friends and admirers of Mr. Romanes (and they are many) will peruse with renewed pleasure, not indeed unmixed with sadness, but one which the general reader will be glad to see rescued from the comparative oblivion of bound volumes of Reviews.

*Diseases of Plants Induced by Cryptogamic Parasites.* By Dr. Karl Freiherr von Tubeuf. English edition by William G. Smith, B.Sc., Ph.D. Three hundred and thirty Illustrations. London, New York and Bombay: Longmans, Green and Co., 1897.

The study of Plant-pathology is one which has been almost neglected in this country, and yet from a practical point of view it undoubtedly ought to be regarded as of great importance. The comparative oblivion under which it is suffered to remain is partly due to the somewhat academic fashion in which Botany is chiefly pursued in England, and this again is brought about by the useless but none the



less burdensome pressure of the examination system which gives scant encouragement to wander into branches of study requiring the expenditure of much time in the field—time which could be so far more economically and profitably (!) employed in getting up facts from books and lecture notes, or in poring over sections in a laboratory.

And indeed there is little enough to stimulate any one in this country to undertake this kind of work. We are a “practical” people, and we show our appreciation of the value of scientific help by allowing our forests, in many cases, to get on as best they can under a mere rule of thumb management. This course however has at least the merit of providing those who care for such things with museums of mismanagement on a not inconsiderable scale.

But in Germany they conduct things better. There forestry is a serious pursuit, and the scientific assistance rendered to the forestry departments by a properly trained staff of pathologists and botanists working in suitably equipped institutions is appreciated as a matter of the highest importance to an industry which is conducted on a purely commercial—and remunerative—basis. There is no reason why silviculture should not pay equally well in this country if its rudiments were but understood.

Much of the land now lying idle as the result of conditions of agricultural depression which are not likely to be materially ameliorated, might profitably be afforested, but it is of little use to go in for new planting in the ignorant and blindly stupid fashion which is only too prevalent in matters relating to landed affairs in England. “Where the carcase is, there will the eagles be gathered together,” and where a forest is there will always be diseases of various kinds to combat. A successful issue to the struggle can only depend on the intelligent application of remedial measures based on an accurate knowledge of the structure and constitution both of the trees and their enemies.

The translation of von Tubeuf’s book will, at any rate, make clear to those persons who are disposed to think at all on these matters, that the subject of Plant-disease is a large one. The author expounds in the introduction the general nature of fungal parasites and saprophytes, and their relations to their living or dead hosts as the case may be. It is tolerably certain that his views on some of these matters will not secure very general acceptance; this, however, does not affect the value of the second and far larger part of the volume in which he treats of the individual fungi, indicating their method of attack, and the kind of damage they effect. Remedial measures are also often suggested for particular cases.

The work is illustrated by a large number of figures and photographs. The latter, however, can hardly be praised; indeed, they are often so badly reproduced as to be almost valueless. But in spite of this, we can confidently say that every one who is at all interested in these questions ought to have the book in his library. Many persons who would find it difficult or tedious to read the original will be grate-

ful to Dr. Smith for his translation, which, if rather laboured at times, appears on the whole to be well and accurately done.

*Smaller Atlas of Illustrations of Clinical Surgery.* By Jonathan Hutchinson, LL.D., F.R.S. London: West, Newman and Co.

Mr. Jonathan Hutchinson's original *Illustrations of Clinical Surgery* in folio size, in two volumes and in price almost prohibitive has been more frequently a source of envy to those who could not afford to buy it than a joy to the envied few who could afford to do so. By the publication of the *Smaller Atlas*, a work dealing with similar but not the same subjects, by reason of its modest price, the possibility of possession is extended to the many. As in the case of the larger *Atlas*, the series of illustrations is conducted on no fixed and systematic lines; it is merely a collection of pathological curiosities, and, as Mr. Hutchinson remarks, he has selected what interested himself in the hope that it would interest others. Those who have attended his clinical *séances* and those who have examined the specimens in his clinical museum and are thus familiar with his presumable interests will have little doubt as to the great intrinsic value of this compilation. Others who from want of time or opportunity are debarred from personal attendance or examination will derive some secondary fire and enthusiasm for matters pathological by an inspection of the beautiful illustrations collected in the *Atlas*, and from reading the lucid explanatory letterpress interpolated between the plates. The latter are 136 in number and mostly coloured, and although chiefly illustrative of skin conditions they include many of general pathological interest. Medical men who have been unable by reading and clinical experience to keep themselves abreast of modern pathology will find these illustrations of skin conditions especially valuable. The older nomenclature has given place to a new order of things, and a conservative adherence to old names for old diseases is often accounted ignorance by those who have derived their learning in more modern schools.

*Metals.* By Huntington and McMillan. New Edition. Longmans Green and Co. 7s. 6d.

This book is based upon the work originally compiled by the late Prof. C. L. Bloxam in 1872, and re-edited and enlarged by Prof. Huntington in 1882.

The present edition has been still further enlarged, and for the most part brought well up to date, under the joint authorship of Prof. Huntington and Mr. McMillan. In its present form, the book, although not full enough to satisfy the requirements of students who are taking up metallurgy as a speciality, will be found of great use to the chemical student and others who are desirous of gaining a rather



fuller knowledge of the details and technicalities of metallurgical processes than are to be found in chemical text-books. The methods of "Coking" have been brought well up to date by the introduction of a description of the newest form of Semet-Solvay oven; and the section devoted to gaseous fuel and regenerative furnaces is much to be commended. It is to be regretted however that with the exception of a somewhat scant description of the electrical method for the production of aluminium no mention is made of this most modern of metallurgical engines, the electric furnace.

*Die Morphologie und Physiologie des pflanzlichen Zell Kerne Eine Kritische Litteraturstudie.* Von Prof. Dr. A. Zimmermann. Mit 84 Figuren im Text. Jena: Verlag von Gustav Fischer, 1896.

The author of this work has laid the general Botanical, and indeed Zoological, public under a debt of gratitude by producing an epitome of the multitudinous papers which have appeared on the subject of the vegetable cell-nucleus. We say *Zoological* public advisedly, because the results of their co-workers in the field of vegetable cytology are too often ignored by those who make animals their special study. But if there is one fact which stands out more clearly than another in the history of modern cytological investigation, it is this one, namely, that it is impossible, as well as unprofitable, to generalise either from the purely animal or the purely plant side in these inquiries. True it is that the partnership between Botany and Zoology has long ago become practically divorced, but that was but the inevitable consequence of the divergent paths followed in the evolution of the respective subjects of the two sciences. But the Protoplasm and Nucleus are structural entities common to both, and the conclusions arrived at on the two sides demand mutual completion and, not less, mutual checking. It is difficult enough to generalise soundly as it is, without going out of our way to avoid utilising the means of assistance which are accessible.

Dr. Zimmermann's book is one which will prove of great use as a guide to the literature on the plant side. It is very thorough, and on the whole seems remarkably free from the mistakes which it is very difficult to exclude from such compilations.

An account is given of the various histological methods in common use, together with their direct application to the study of the nucleus. The structure of the latter is discussed, and its behaviour during division is fully described. A few pages are devoted to a consideration of the physiology and function of the nucleus.

In the special part of the book, the nucleus is treated of as it occurs in plants belonging to the various divisions of the vegetable kingdom, and many interesting facts are here brought incidentally under review. An admirable bibliography forms by no means the least valuable feature of what we are glad to be able to characterise as an extremely useful book.

*The Cell in Development and Inheritance.* By Edmund B. Wilson, Ph.D. The Macmillan Company. 1896.

Professor Wilson's work is a clear and vigorous history of a province of biology which has become far better known and more interesting to the general scientific reader since the publication of Hertwig's Work, *Die Zelle und die Gewebe*. And it is perhaps not to be regretted that this new treatise on cellular biology is written from a decidedly Boverian and Weismannistic standpoint. Such a method brings out the cardinal points of the subject in far sharper outline before the general reader, than would be the case with any amount of analytical treatment, though this latter might be better adapted to the requirements of the few.

The introduction and the chapters dealing with the general characters of the cell—cell division—and germ cells, are all excellent, although in the description of the Mitotic Evolution perhaps undue importance is given to the centrosome as a cell organ. The general drift of experience seems rather to show that this structure is more the expression of the operation than the controller, of the intracellular forces.

The chapter on the conjugation in unicellular organisms is particularly good, and is in fact by far the most lucid *résumé* of the observations made on this complex subject, which is in existence.

It is only when we come to the chapters dealing with the vexed question of chromatin reduction in the generative cells that the work appears to be in any way open to serious criticism. The subject is at the present time entirely *sub judice*, and the attempt to treat it from a pronounced Weismannistic standpoint necessarily leads to an inflation of the importance of some observations, and the suppression of that of others, which is decidedly objectionable in our present state of knowledge. This is particularly apparent in the way the Author brings forward vom Rath's work on Salamander as lending much support to reduction in Weismann's sense, because this work has recently been shown by Meves<sup>1</sup> to be quite unsound.

The Spermatogenesis in Salamander completely corresponds with that described by Moore in Elasmobranchs and with Brauer's interpretation of the same phenomena in *Ascaris*. It is thus apparent that whatever the value of the process described in Copepods by Häcker, may eventually turn out to be, the universality of the "reductionstheilung" does not at present hold. The argument as based on the results of vegetable cytology is marred by the fact that the author does not always appear to be clear as to the standpoint of the authors he quotes, and in one such instance the respective facts are actually transposed; in fact throughout this chapter the author's endeavour to maintain his standpoint, although persistent, strikes us as being rather prejudiced.

<sup>1</sup> Ueber die Entwicklung der Männlichen geschlechtszellen von *Salamandra maculosa*. *Arch. f. Mikr. Anatomie*, Bd. 48. 1896.



The immediately succeeding chapters contains a complete description and classification of cell organs into persistent and non-persistent types of the different forms of spheres, and much interesting matter relating to the other constituents of the cell. In chapter viii we find a full description of "cell division and development" and in the succeeding chapters there is a very clear and readable discussion of the several theories of development, through all of which the author's own special knowledge is utilised in full, as in the passages dealing with the nature and causes of differentiation, the Promorphological relations of Cleavage and many more.

The whole work thus forms a most useful *résumé* of a large subject, the literature of which is so voluminous that it continually threatens to obscure the contained substratum of observations, and an epitome of this sort is a most important acquisition, as it brings the questions which legitimately spring up, when all the observations in each department are taken together, clearly into view.

*Der Lichtsinn augenloser Thiere.* Eine biologische Studie. Dr. Willibald Nagel. Jena: Gustav Fischer, 1896.

The author here reprints an interesting and useful lecture on "Sight without Eyes". This lecture, which takes up 48 of the 120 pages of his work, is, as the title signifies, a general account of what is known as the dermatoptic function. The second part gives a detailed account of the author's experiments on Molluscs, which, though blind (naturally or artificially), exemplify this function by reacting in various definite ways to the light stimulus. The third part is made up of appendices which are expansions of important points dealt with too briefly in the lecture. The work closes with a useful bibliography of some eighty references dealing with the physiology of sensation, chiefly of light. These range from Johannes Müller's classical *Zur vergleichenden Physiologie des Gesichtssinnes* (1826) to the author's own recent contributions.

From this outline of the contents it will be seen that the work does not pretend to be much more than a review and discussion of facts already known, *viz.*, that certain lower forms of animals without eyes have acquired the power of reacting to sudden changes in the intensity of light. As such, however, it is timely and interesting. Biologists will be grateful to the author for pointing out the interesting fact that those animals which possess hard, protective shells into which they can retreat and defy their enemies mostly react to sudden diminutions of light, *e.g.*, to passing shadows, such shadows no doubt warning them of the approach of a foe. On the other hand, animals which generally live under sand, from which they occasionally emerge, react on sudden brightenings of the light. The author distinguishes between these two different nerve reactions by the use of the words *Lichtempfindung* and *Schattenempfindung*.

The title of the work is certainly happier than the title of the lecture on which it is founded. It is quite true that both words "sight" and "eyes" are only sharply definable when used of human sight and eyes, and that, when the lower forms of organs for appreciating variations in light intensity are brought into line, the terms are often of more than doubtful applicability. But we do not think that this uncertainty as to what the comparative anatomist and physiologist, as apart from the human anatomist and physiologist, means by sight and eyes justifies the author in applying either term to the sensitiveness of certain skins to light. This, indeed, the author recognises, for on page 18 he modifies the word *Sehen* into *Lichtsinn*, and rightly adopts this modification for the title of his book.

Most people would be inclined to affirm that as the word "sight" was already in use, its meaning was fixed before we had any knowledge of the simpler eyes of the invertebrates, and that, while there can be no objection to calling all organs for the appreciation of light sensations "eyes," we cannot say that all the eyes *see* unless, from their possession of a dioptric apparatus or otherwise, we can conclude that they are capable of appreciating external form-differences.

The author writes as an authority, and all that is at present known of the remarkable sensitiveness to light possessed by the skins of many lower invertebrates (the list of which, by the way, he has not exhausted) he discusses with knowledge and ability. His treatise makes it perfectly clear that we are just as much in the dark as to the real causes of these diffuse light sensations of certain skins as we are of the true causes of the light sensation of our own specialised organ of vision. It is interesting to note that many of the surfaces sensitive to light, *e.g.*, the siphons of *Psammobia*, the skin of a "decapitated" *Amphioxus*, are absolutely free from pigment, but nevertheless the author admits that pigment must have some definite connection with sight, inasmuch as it is always present in specialised visual organs, except in albinos, which are abnormal ("Missbildungen"). As to what this connection is, the author merely repeats the old suggestion that it prevents diffusion of the light rays by sheathing the visual cells, in order that they may clearly distinguish separate points of light. On the other hand, it may be pointed out that it is also always present in eyes which do not "see" in the restricted sense above sketched, and which do not require to distinguish separate points of light.

*Cellulose.* An outline of the chemistry of the structural elements of plants, with reference to their natural history and industrial uses.  
By Cross and Bevan. Longmans.

An almost inevitable result of the increasing activity of scientific investigators of the present day, and the consequent accumulation of scientific literature in almost every department, is the need for the appearance of definite monographs, in which, by specially qualified hands, the vast amount of crude material scattered here and there may



be concentrated into a more compact form, and so presented to the general reader. Messrs. Cross and Bevan in the present volume have brought together the sum total of the work done in recent years on cellulose, and have furnished a monograph, valuable alike to the chemist, the vegetable physiologist, and the reader interested specially in the economic questions associated with this substance.

But though at the outset entitled to great credit for so important a contribution alike to science and to art, it is to be feared that the gratitude of their readers will be largely tinged with other sentiments, for the subject-matter is handled in a manner which is far from attractive. The book, though teeming with information, is emphatically dull, and likely rather to be used for reference purposes than to take its place among technical text-books.

The authors open their work by a somewhat exhaustive discussion of the characters, both chemical and physical, of the typical cotton-fibre, which is the purest form of cellulose known. They examine closely the behaviour of this body with numerous re-agents with the view of elucidating, as far as they can, the composition of its molecule. The results obtained, however, both by themselves and by other investigators, do more at present to show how extremely complicated the whole question is than to give us very definite information.

Dealing with the problem of the synthesis of cellulose they put forward the view that it is built up of molecules of simpler carbohydrates, and they quote two processes which throw some light upon the subject. When the juice of the beet is extracted and allowed to stand for some time a change takes place in it apparently spontaneously, resulting in the separation of lumps or clots of a white insoluble substance which has all the characteristics of cellulose, and when this is separated by filtration, the solution gives with alcohol a gelatinous precipitate which resembles the hydrates of that body. If the lumps first noticed are transferred to a solution of pure cane sugar a further formation of cellulose can be observed. The process is sometimes attended by the evolution of carbonic anhydride and by the formation of a certain amount of acetic acid. It is suggested that the process is due to the action of an enzyme allied to diastase.

The second process of synthesis is due to the action of an acetic ferment, which has been described by A. J. Brown in the *Journal of the Chemical Society*. The organism is composed of bacterial rods which are contained in a membranous envelope. Cultivated in solutions of levulose, mannitol and dextrose, it produces a vigorous growth composed of the bacteria enveloped in a "collecting medium" of cellulose. Levulose seems to be the most useful antecedent.

The interest of the vegetable physiologist will be perhaps most excited by the chapters on the so-called "Compound Celluloses". Of these the authors discuss the ligno-celluloses, pecto-celluloses, muco-celluloses, and adipo- and carbo-celluloses. The modifications of the cell wall which are especially characteristic of wood, mucilage, and cork, have of course

very great importance from their relationship to the physiological division of labour of which the plant tissues are the seat.

The authors go very exhaustively into the relation of these bodies to pure cellulose and establish the view that the latter is the antecedent of them all, being converted chemically into them. The hypothesis therefore of the formation of lignin, suberin, etc., in the cell and its wall becoming impregnated with them by some kind of infiltration is no longer tenable. The question, however, of the details of the transformations, or even whether they came from pure cellulose or some compound built up with it in the ordinary course of elaboration, the authors prefer for the present to leave undecided.

Perhaps the most interesting part of the volume, both to the student and the general reader, is the section dealing with the applications of cellulose in the arts. To the former class of readers, pages 243-273 will appeal very strongly, as the authors give very valuable laboratory and research notes dealing with the separation of cellulose from the various vegetable tissues, the methods of analysis, the characters of cellulose compounds, etc. The latter portion of the volume is more adapted for general reading, as it embraces a summary of the economic uses of the material. Many of the criticisms of the writers on these points are of the greatest value, particularly the section devoted to the consideration of the manufacture of paper from different celluloses. A fuller examination of these points is beyond the scope of the present notice, but the section in question brings out very grave considerations as to the permanence of many of our records.

The book is illustrated by fourteen plates which are reproductions of microphotographs of sections showing the sources of most of the celluloses of commerce.



## APPENDIX.

### NOTICES OF BOOKS.

*Catalogue of the African Plants collected by Dr. Friedrich Welwitsch in 1853-61. Dicotyledons, part i.* By William Philip Hiern, M.A., F.L.S. London: Printed by order of the Trustees of the British Museum, 1896.

The late Dr. Welwitsch was not only an accomplished botanist, he was a most discriminating and painstaking collector, and his collection of some 5000 species of Angola plants was a monument of skill and industry. It was a model of neatness and order, and most of the species were represented by a numerous series of specimens, accompanied by copious descriptive notes and observations made on the spot. The preparation of this herbarium occupied him upwards of seven years, and was accomplished under great difficulties and privations, to say nothing of severe attacks of fever and other diseases which few travellers in tropical Africa escape. He travelled in the service of the Portuguese Government, and in 1863 was permitted to come to England to work out his collections. The remainder of his life was devoted to this purpose; yet he published comparatively little; partly in consequence of the extremely critical nature of his work, and partly in consequence of almost continuous bad health. He died in 1873, and after some litigation with the Portuguese Government, his executors secured a very full set of his plants and a transcript of all his notes for the British Museum. Soon after Dr. Welwitsch settled in London Professor D. Oliver's *Flora of Tropical Africa* was commenced, and Welwitsch generously allowed the use and incorporation of his plants—almost the only ones known from Lower Guinea. This was continued, though imperfectly, through volumes i. and ii., and then interrupted.

Mr. Hiern's *Catalogue* is the first part of a work intended to embody Welwitsch's notes and descriptions, and his own descriptions of any unpublished species he may find in the course of his investigations. The part issued includes the orders Ranunculaceæ to the Rhizophoraceæ. It is preceded by a portrait and biographical sketch of Welwitsch, and a bibliography of his published writings and of other writers' publications, exclusively or chiefly devoted to definite parts of Welwitsch's collections. That Mr. Hiern has done his work very thoroughly is no more than would be expected from his previous performances; but there appears to be no mention of the language in which the notes and descriptions were originally written. This was Latin, and it is a question whether it would not have been better to have published them in the original, seeing that the collections were distributed among the herbaria of various countries. However, it is a great thing to have this treasury of informa-

tion accessible to the world. "Catalogue" must be regarded as an official rather than appropriate title, inasmuch as the compiler himself contributes descriptions of seventy new species and two new genera. The latter are *Epinetrum*, an imperfectly characterised genus of Menispermaceæ, of which only the male flowers are known; and *Zanha*, Burseraceæ. With regard to nomenclature, Mr. Hiern is a staunch follower of Dr. O. Kuntze, except where we can find an older name, no matter how obscure or barbarous; but there is no doubt a sincere attempt at consistency, and, as current names are cited, it is not so difficult to follow as some recent American works, in which obscure names replace familiar ones in the absence of synonymy.

*A Manual and Dictionary of the Flowering Plants and Ferns.* By J. C. Willis, M.A. Vol. i. (pp. xiv., 224) = part i. Vol. ii. (pp. xiv., 430) = part ii. Cambridge Natural Science Manuals. University Press, 1897. 10s. 6d.

This book may be said to consist of part ii. and part i. The author found, as he tells us, that part ii. (the Dictionary) was "wanting in co-ordination," and so wrote part i. (the Manual) "to supplement it". One hardly expects to find "co-ordination" in a dictionary, nor is it easy to see how this quality can be introduced by writing "a kind of index" to the said dictionary, even when this co-ordinating supplement or "kind of index" evolves during the writing into "what is practically a text-book of morphology, classification, natural history and geographical distribution". But let us leave the logical peculiarities of the book's inception and endeavour to judge each part on its own merits. Part ii., then, is intended to supply in the dictionary form "as much information as is required by any but specialists, upon all those points—morphology, classification, natural history, economic botany, etc.—which do not require the use of a microscope". Now the want of a book of this kind has been felt by botanists for some years, and part ii. of the present work certainly goes some way towards supplying it. The only question is whether it would not be a great deal more valuable as a book of reference for botanists if it were very considerably larger. But it appears that the author has particularly in view the needs of the elementary student "when placed before the bewildering variety of forms in such a collection as that at Kew," and these necessitate the restriction of the work "within a reasonable compass". Of course it is very easy to criticise such a work from an adverse standpoint—omissions there are which we should like to see repaired, but on the whole the book (*i.e.*, the second volume) will, without doubt, abundantly justify its existence, and prove a great boon to all those for whose help it has been written.

Part i. has to be judged on a very different footing. It is supposed to be intelligible to "any one who has studied any of the small elementary treatises on Botany," and chapter i. (more than half the volume) is avowedly intended to be read by a student in his first year of botanical



study. The amount of information crammed into the hundred odd pages of closely printed matter (relieved by but one solitary diagram) contained in the first chapter is positively appalling; nor can the lucidity of the author's style be said to compensate for the congestion of his matter. We cannot refrain from quoting an example in justification of this remark. Aerial roots, the author says, "are usually formed upon stems or leaves; such roots, together with branch roots formed upon other roots but not in acropetal succession (see below), are classed under the term of *adventitious roots*, whilst the original root derived from the embryo together with its normal branches (those formed in acropetal succession) are spoken of as *true roots*" (p. 21). We heartily condole with the student who attempts to assimilate this clumsily prepared morphological pemmican. And to make the matter worse, the author by no means confines himself to boiling down matters of fact and of accepted morphological doctrine, but under the plea of giving life to the dry bones of morphology by an "evolutionary" treatment, he introduces a large amount of highly speculative matter which does not escape the necessary dogmatism of the whole.

Of inaccuracies there are, as was to be expected, but few; and those almost entirely where the author ventures upon ground which he has wisely forbidden himself in the Preface—namely where he discusses topics which "require the use of a microscope".

The part of chapter i. dealing with the "Natural History of the Flower," and chapter iii., which deals mainly with "biological" groups of plants, contain useful if somewhat disjointed summaries of existing knowledge on these subjects; and the same remark may apply to that part of chapter ii. which deals with the "Principles of Classification". But we must protest against the section on "Variation" in this chapter. There was no need for the author to attempt to give an account of the methods employed in the statistical study of this subject, but having done so he might have taken the trouble to avoid the misstatements and confusions which literally crowd the single page devoted to this topic.

It is to be hoped that in future editions we may see part ii. somewhat expanded, and issued by itself, for we cannot approve the scheme of part i. (entirely apart from the question of its execution). If the author wishes to write a treatise on certain branches of botany, let him devote the necessary time and thought to its production. An adequate treatment of the subjects indicated in the preface would fill at least three times the space which the writer has given them. But do not let him imagine that he is benefiting anybody, least of all the elementary student, by writing what we must reluctantly call a cram-book on some of the most fascinating and important topics in the range of modern botany.

*Estudios sobre la Flora de las Islas de Juan Fernandez.* Por Federico Johow. A espensas del Gobierno de Chile. Santiago de Chile. Imprenta de Cervantes, 1896. 4to, pp. xi. and 287, with two maps, eight engravings in the text, and eighteen plates.

This is a valuable contribution to the literature on Insular Floras;

its value depending almost entirely upon the fact that it embodies the results of actual observation, instead of being drawn up from herbarium specimens, supplimented by the more or less imperfect notes of collectors.

With regard to numbers of genera and species, it contains very little that is not in Hemsley's account of the Flora in the Botany of the *Challenger* Expedition. But it embodies all that that contains, with very much additional biological, local geographical, and historical matter. It has the double advantage of being a consolidation of the work of a botanist who had access to Bertero's types and all previously existing literature, with that of a botanist whose investigations were conducted in the field. The author draws largely on Hemsley for synonymy and general geography, and is careful to cite his authority in every instance. The enumeration is preceded by an account of the geography and geology of the islands; a somewhat detailed history of their botanical exploration; and a full and interesting bibliography; and it is followed by an analysis of the flora; a description of the vegetable formations; catalogues of the insects and birds; and an appendix on the products of the animals, and the management and conservation of the woods and plantations. Dr. Johow has reduced a number of doubtful species, and in return he describes about half a dozen as new. Notable amongst the latter are *Centaurodendron dracænoides* and *Dendroseris gigantea*. The former is remarkable in the tribe *Cynareæ* for its aboreous character, and the latter for its size—up to twenty feet high, among the cichoriaceous arboreous Compositæ. The total number of endemic species of vascular plants resulting from Dr. Johow's elaboration is sixty-nine as against seventy given by Hemsley; and these belong to fifty-two genera, whereof twelve are endemic, and to thirty-two natural orders. In addition, there are seventy-four indigenous but not endemic species. Reference has been made in SCIENCE PROGRESS<sup>1</sup> to the sandalwood tree of Juan Fernandez. Dr. Johow succeeded in finding one tree, after weeks of fruitless searching.

The beautifully executed plates, illustrating the scenery and characteristic types of vegetation add greatly to the interest and value of the book.

*The Theory of Sound.* By Lord Rayleigh. Second edition, revised and enlarged. 2 vols., 480 + xiv., and 504 + xvi. pp. London: Macmillan & Co., 1894 and 1896.

There are three works in the English language on Natural Philosophy which occupy quite a unique position; these are Maxwell's *Electricity and Magnetism*, Kelvin and Tait's *Natural Philosophy*, and the work under notice. For in every branch of physics which has so far progressed as to be treated by the methods of the mathematician we continually make use of the results and investigations contained in

<sup>1</sup> I., p. 401.



these three books. There is another striking resemblance between them in that in each case while free use is made of the help of mathematics the *physical* bearing of the problems and the *physical* interpretation of the results is everywhere given a prominent place.

In a notice of the first edition of Lord Rayleigh's *Sound* von Helmholtz concludes as follows: "At the end of the volume Lord Rayleigh has placed the words 'The End'. We only hope that this may be only the provisional, not the definite end. There is still an important chapter wanted, *viz.*, that on the theory of reed pipes, including the human voice. . . . After reed pipes we would mention the theory of singing flames and the blowing of organ pipes." In this second edition we have a fulfilment of Helmholtz's wish, for in the three hundred and fifty odd pages of additional matter the author has included discussions on these points.

The first edition is so well known to all physicists that it will only be necessary to refer to the additions which have been made in this edition.

Throughout the volumes short paragraphs and steps in the mathematical reasoning have been here and there added, and what is of much importance references to recent works on the subject have been included. The first considerable addition is a discussion on the vibrations of bells, in which the author describes the results of the experiments he has conducted in this subject. He has examined a number of church bells, determining in each case the different tones the bells are capable of yielding, and has been led to the interesting result that in English bells it is the fifth tone in order which agrees with the nominal pitch of the bell, while in Belgian bells it is the second tone that agrees with the nominal pitch. The author then goes on to investigate the vibration of curved plates and shells, the theory being only strictly applicable when the thickness is infinitely small.

From the author's well-known investigations on the telephone one naturally looks for a chapter dealing with this instrument; and in this connection there is also one on alternating currents, including the passage of alternating currents through a network of conductors, and the resistance of conductors to alternating currents. In connection with the measurements of the current needed to give an audible sound in a telephone given in the text, and also with reference to the minimum amplitude of sound waves that are audible, it is interesting to recall some recent measures by Barus who showed that the amplitude of the excursions of a telephone diaphragm is less than  $10^{-6}$  cm.

Two very interesting sections are added dealing with the repulsion of resonators and the attraction between a vibrating body, such as a tuning fork, and a light suspended body. Incidentally the author considers the tendency of a suspended disc to set itself at right angles to the direction of alternating currents of air. Boys has shown to what an extraordinary degree the sensitiveness of such a disc as a detector of response in a resonator can be carried, and it is rather astonishing that

this arrangement has not been used in connection with a series of resonators to estimate the *intensity* of the overtones of notes produced by various instruments. The author in this section also gives an account of A. König's explanation of the transverse ridges in which cork filings in a Kundt's tube set themselves. The explanation depends on the fact that two spheres at a moderate distance apart in an alternating current will, on account of the difference in the velocity of the air between them and that along their averted hemispheres, repel one another if the line joining the centres is parallel to the direction of motion of the air, and will attract one another if the line joining the centres is perpendicular to the stream of air. The result of these forces being a tendency to aggregate in transverse laminæ.

In the chapter dealing with the vibration of organ pipes the author, while mentioning the observations made by Töpler and Boltzmann, in which the optical interference between two rays of light, one passing at the side of the pipe and the other through the air in the pipe, which, on account of the vibrations, is alternately compressed and rarified, does not mention the beautiful results obtained by this method by Raps (*Wied. Ann.*, 50, 193, 1893).

The subject of singing flames and such like, in which the vibrations are maintained by heat, is a most fascinating one. The complete explanation of the phenomena on account of the peculiar and ill-understood behaviour of the flames being a matter of considerable difficulty. The author discusses Sondhauss's experiments in this subject, and shows how the effects may be explained on the supposition that stationary vibrations are set up in the gas supply tube, the phase of which may be either the same or opposite to that of the vibrations in the resonator. Since it is probable that the greatest development of heat is slightly retarded in comparison with the issue of gas, there will be a tendency, according to the difference in phase, either to maintain or to damp out any existing vibrations in the resonator. The vibrations set up in glass bulbs when heated, a phenomenon familiar to all glass-blowers, is another example of vibrations maintained by heat, and in this connection the author might have considered the very interesting thermal engine exhibited, we believe for the first time, by Mr. Griffiths at the meeting of the Physical Society held in the Cavendish Laboratory a year or two ago. It consists of a glass bulb about 6 cm. in diameter connected to a U-shaped tube of about 1 cm. bore. The U is filled with mercury for about 6 cm. up each limb and the bulb heated over a flame. If the mercury is disturbed by plunging a rod into the open limb of the U, oscillations are set up which increase in amplitude to a most astonishing extent, and are maintained as long as the heating continues.

The additional chapters, to which we have not space to refer in detail, deal with the effects of friction and heat conduction on acoustical problems, capillarity and capillary waves and ripples, vortex motion and sensitive jets, vibrations of solid bodies, and finally a long chapter



entitled facts and theories of audition. In his preface the author states that this last chapter has entailed labour out of proportion to the results, but here we do not agree with him, and fancy that in this all students of Physics will agree with us.

A notice of such a work as Lord Rayleigh's must of necessity partake of the character of a table of contents for the only thing that can really be said about it is to regret that the work is not larger, and to express a hope that the author will himself attack some of the problems which he indicates as awaiting a satisfactory solution.

In conclusion we need only say that this edition is practically the publication of a third volume and must be invaluable to all physicists.

*Magnetic Fields of Force.* By Professor H. Ebert. Translated from the German by Dr. C. V. Burton. Pt. i., pp. xviii. + 297. London: Longmans, Green & Co., 1897. 10s. 6d. net.

In this volume the phenomena of magnetism and electricity are developed according to Faraday's conception of lines of force. In Maxwell's famous book on this subject the advanced student possesses a complete treatise; to those, however, who have not got a great command of mathematics this work is of very little use. In Professor Ebert's book we have the subject dealt with in a clear and concise manner and without the assistance of any mathematical reasoning which is above the understanding of a student acquainted with quite the elements of this subject. In part i. the more elementary portions of the subject are dealt with, the consideration of the phenomena of induction, single and multiphase periodic currents and electrical oscillations being reserved for a subsequent volume.

Throughout the volume directions are given for performing experiments suitable for lecture demonstration, or for the use of elementary students in the laboratory. These directions are rather detailed and in most cases are easy of performance. On page 97, however, in *Experiment* No. 40, the reader is told to suspend a magnetic needle by fastening to its middle a fine fibre, and is told that it will set itself in the direction of the earth's magnetic lines of force, no warning being given as to the difficulty which would be encountered in avoiding the disturbing effect of gravity if the needle is not supported exactly at its centre of gravity. The experiment then proceeds: "Now disturb the needle from its position of rest and allow it to oscillate. From the frequency of oscillation we can calculate  $T$ , the resultant intensity of the earth's magnetic field, or *total force*." This is quite wrong if we take it literally, as from what is said in the next section about deriving the value of  $H$  from that of  $T$  obtained as above, or if the author means that from the period of oscillation *and the value of the dip*  $T$  can be calculated we can only say he has managed very successfully to obscure his meaning.

In a work such as this where all the magnetic phenomena are considered as due to something going on in the ether it is rather

astonishing to find that all the dimensions are given subject to the assumption that the permeability of the medium is without dimensions being merely a ratio. The inclusion of the permeability and specific inductive capacity in the dimensional equations seems as if it would never find its way into any elementary text-books.

The translation is everything that could be desired, the English being clear and not defaced by the German construction of the sentences so often found in translations. Dr. Burton has added here and there explanatory sentences (indicated by square brackets). In one or two places, however, these additions might have been considered as *corrections* and introduced into the text, for at present there are a few rather laughable sentences formed by the combination of the translator's addition with the author's original statement. Thus on p. 277 we read: ". . . A current of one ampère produces at a distance of 1 cm. from its axis a field-intensity of  $\frac{1}{5}$  of an absolute unit, supposing the permeability to have the value unity [or any other value]".

*Physiologische Pflanzenanatomie*, von Dr. G. Haberlandt, O. Ö. Professor der Botanik, vorstand des Botanischen Institutes und Gartens a. d. k. k. Universität Graz. Zweite, neubearbeitete v. vermehrte auflage, mit 235 Abbildungen. Leipzig, Wilhelm Engelmann, 1896.

The publication of Dr. Haberlandt's *Physiologische Pflanzenanatomie* some twelve years ago marked a new departure in the general treatment of anatomical facts. Naturally the author did not himself actually initiate the movement of which his book was the outcome, but he was perhaps the first who gave a clear and general exposition of the old facts regarded from the new standpoint, and the results have fully justified his efforts. Anatomical characters, no doubt, oftentimes possess an intrinsic importance of their own, even from a taxonomic point of view; that is, they may possess even a high value in certain cases, as in a measure indicating phylogenetic affinities. But no one will deny that in the vast majority of cases one is on very unsafe ground in attempting to show phylogenetic conclusions from such a source. And this being so, it is obvious that plant anatomy is in some degree robbed of an interest which renders the study of the comparative anatomy of animals so interesting. But, on the other hand, the botanist gains on account of the great extent of individual (*i.e.*, within the same species) variation exhibited by plants, and the marked correlation which may be seen to exist between the organism and the special kind of environment in which it happens to be located. A plant cannot often grow where it will but where it must. Hence the continuous need of a possibility of variable response to conditions which themselves vary. Thus it is that plant anatomy is so closely bound up with the circumstances of the passive environment, and that its study, from this point of view, constitutes one of the most fascinating branches of investigation, although the ulterior question as to how it is possible for an organism to have become possessed of the power of responding in a purposeful



way to this *or* that set of conditions is still a mystery, and is long likely to remain so in spite of the assurance to the contrary of sundry writers on these matters.

The new edition of Professor Haberlandt's work is a greatly enlarged and in most respects a greatly improved one. The fact that the author has himself contributed in no small degree to our knowledge of the subject imparts to his book a freshness, and an interest to his method of treatment which only a first-hand acquaintance with the facts can give. Moreover, Dr. Haberlandt knows when he has said enough on any topic, and does not weary his reader with tedious detail, but rather stimulates him to prosecute further researches for himself.

Without doubt the book in its present form will, as it thoroughly deserves, enjoy a wide reputation, safe of welcome recognition at the hands of all who are competent to form an opinion as to its merits.

*The Ancient Volcanoes of Great Britain.* By Sir Archibald Geikie, D.C.L., F.R.S., etc., Director-general of the Geological Survey of Great Britain and Ireland. 2 vols., pp. 477 and 492 with 7 maps and 383 illustrations. Macmillan & Co., 1897.

It is impossible to rise from the perusal of this work without being impressed alike by the prodigious industry of its author and by the remarkable literary skill with which he has utilised the vast mass of materials that he has collected. The work, which as now presented to us is almost encyclopædic in character, is an expansion and development of two valuable addresses delivered by Sir Archibald Geikie in 1891 and 1892 as president of the Geological Society, and of a memoir on the Tertiary Volcanoes of Britain contributed by him to the Royal Society of Edinburgh in 1888.

During his long connection with the Geological Survey, and in the course of his labours in mapping portions of our islands, especially in Scotland, the Director-general has enjoyed special opportunities, as he informs us, for studying the numerous rocks of volcanic origin associated with the whole series of British strata. In the present work he has brought together his own observations with those of his fellow-members of the Survey, and of other geologists, bearing on the history of Volcanic action in the British Islands, and he has combined the whole with such striking literary ability as to make the work as readable and intelligible as it is accurate and painstaking. Nor is the book, though avowedly based on publications already familiar to geologists, wanting in original matter; many new observations—especially those made during a yachting cruise in the Western Isles of Scotland—with numerous fresh illustrations and not a few valuable contributions from the field-geologists, palæontologists and petrographers of the Geological Survey repay the readers of this book who are already familiar with the author's earlier publications. An especially valuable feature of the book consists in the number and accuracy of the references to the original sources of information which it contains.

The first division of the work, running to somewhat over one

hundred pages, is devoted to a general sketch of modern volcanic action and a comparison of ancient volcanoes—as illustrated by their denuded relics embedded among the sedimentary deposits of past ages—with those of the present day. The author then proceeds to sketch successively the evidences of volcanic action in the British Islands, in Pre-Cambrian, Cambrian, Silurian, Devonian and Old-Red-Sandstone, Carboniferous, Permian and Tertiary times. Convenient as is this strictly chronological order from many points of view it is attended with the disadvantage that the writer is compelled to proceed “from the unknown to the known”—from the study of the much altered and greatly denuded fragments of old volcanic rocks, in which the relations with modern deposits are often very obscure to the comparatively fresh and well-preserved relics of Tertiary Volcanoes, in which the analogies with existing volcanic masses are so clear that they cannot be misunderstood. Apart from this obvious objection to his method, however, all geologists must feel indebted to the author for the way in which he has succeeded, by weaving together facts and observations from sources new and old, in giving a connected and up-to-date account of all that is known concerning the volcanic history of Britain during each of these ancient periods.

The last chapter of the work, consisting of about a dozen pages, is devoted to a “summary, and general deductions”. It is here, if anywhere, that the reader may perhaps experience some little disappointment. In the various memoirs on volcanic phenomena—the publication of which has extended, as the author reminds us in his preface, over a period of nearly forty years—it naturally happens that we are able to trace many changes of opinion or rather developments of the author’s knowledge; there is indeed very little in common between the conclusions arrived at by him during the first half of that period and those expressed during the latter half. As Sir Archibald Geikie has frequently to admit in the course of the work, the views he now expresses are, on many points, strikingly divergent from those which he formerly maintained, while certain of those views are in not less marked conflict with the conclusions of some of his contemporaries. Many geologists will, we think, demur to the new analysis and classification of volcanic phenomena presented in the pages of this his latest work. But concerning the great value of the book—embodying as it does a vast amount of original observation, patiently collected by himself and numerous fellow-workers in the same field, and skilfully woven into a connected and amply illustrated narrative of the succession of events in past geological times—there cannot be two opinions. Apart from all theoretical considerations, the author must be congratulated upon having produced a treatise which will be of great and permanent value as a book of reference, and, at the same time, of a literary masterpiece which cannot fail to add to his already high reputation as an exponent of science.



## APPENDIX.

### NOTICES OF BOOKS.

*The Elements of Physics.* By Edward L. Nichols and William S. Franklin. Vol. iii. Light and Sound. The Macmillan Co., 1897.

This is the third and concluding volume of a text-book, the second volume of which was noticed in SCIENCE PROGRESS (April, 1897). In this volume the two branches, Light and Sound, are considered together under the general head of wave motions which affect the sensory nerves. The remarks made with reference to the second volume apply in the case of the third volume, with the exception that in this volume the references have been put in.

*Studies in Chemical Dynamics.* By J. H. Van't Hoff. Revised and enlarged by Dr. Ernst Cohen. Translated by Dr. Thomas Ewan. Amsterdam: F. Muller & Co. London: Williams & Norgate, 1896.

The first edition of Professor Van't Hoff's *Etudes de Dynamique Chimique* being exhausted, the question of issuing a new edition was suggested, but the difficulty arose that the *Etudes* represented the stage of the author's chemical thinking at the time of their publication about twelve years ago, but that now-a-days most thinkers have passed beyond this stage. To make many changes in the new edition would, however, have taken away from the work its desired documentary character, while to change nothing would have contributed nothing towards making the contents acceptable to the public. Under these circumstances Dr. Cohen undertook to revise the *Etudes*, so as to include not only the old matter, but also an account of the researches which have been engendered by it, so as to form a record of the work carried out in Van't Hoff's laboratory.

The book is divided into four sections dealing with (1) the course of chemical change, (2) the influence of temperature on chemical change, (3) chemical equilibrium, and (4) affinity.

In each case, in addition to a complete account of the experiments which have been made, and the apparatus used, there is a theoretical discussion, the experimental facts being used to test the accuracy of the theory. It must not be supposed that the experiments made in Van't Hoff's laboratory are exclusively referred to, references are given to work bearing on the subject done elsewhere, and the results obtained are quoted.

The translation is all that could be desired, and the book will be of great use to English-speaking chemists and physicists both as showing in a clear and striking manner what has been done in the subject, and as a source from which many instructive and probably fruitful suggestions may be obtained.

*The Induction Coil in Practical Work.* By Lewis Wright. pp. 172.  
London: Macmillan & Co., 1897.

The enormous number of induction coils which during the last years have come into general use, the users in many cases having no previous experience in electrical matters, makes the publication of a book giving practical direction as to the use of a coil of some value. Mr. Wright not only describes in popular language the modern induction coil, and the practical details necessary to apply it to the production of Röntgen rays, but also gives descriptions of other experiments which can be performed with such a coil. Thus there are chapters on discharges in partial vacua, spectrum work, and discharges in high vacua. No doubt the book will be found of great service, particularly to medical practitioners who are attempting to apply Röntgen rays to diagnosis.

*Elements of Electro-Chemistry.* By Dr. Lüpke. Translated by M. M. Pattison Muir. London: H. Grevel & Co., 1897.

This work is intended to give those who are not in a position to make an exhaustive study of the subject an insight into the modern theories of electro-chemistry and of the experiments by means of which these theories are supported. The various laws are throughout deduced directly from the result of experiment, and mathematical discussions are only very sparsely introduced. The experiments, which are very fully described, are of the nature more of lecture experiments than of exact quantitative determinations. Hence it follows that the book is more suited as a handbook for use in a laboratory where the students perform elementary physico-chemical experiments, or for the use of a teacher who wishes to illustrate his lectures by experiments, than as a text-book for the use of students anxious to know how the results have been actually obtained.

The first part of the book deals with the modern theories of electrolysis, and in this section we find a consideration of Hittorf's experiments on the velocity of the ions, Kohlrausch's work on the electrical conductivity of dilute solutions, Arrhenius's theory of dissociation. The second part deals with Van't Hoff's theory of solutions, and contains chapters on osmotic pressure, vapour pressure of solutions, boiling and freezing points of solutions, the connections between osmotic pressure, vapour pressure, increase of boiling point and lowering of the freezing point, and on the applications of Van't Hoff's law to solutions of electrolytes. The third part deals with the osmotic theory of the current in galvanic cells. This section includes a chapter on Nernst's calculation of the E. M. F. of cells from the osmotic pressure theory. In the next three chapters, which are on concentration cells, Daniell cells, and reduction and oxidation cells, the formulæ, etc., obtained in the first chapter of this section are applied. There are also chapters on the solution pressure of the metals, intensity of fixation and polarisation, irreversible cells, accumulators, and the energetics of galvanic elements. The last chapter deals with so



important a part of the subject that its meagre and scanty treatment of the subject of energetics is much to be regretted.

Now that chemists are everywhere measuring physical quantities, it seems a pity that they cannot make up their mind to use the C. G. S. system of units in its entirety, so that one would not find work measured in "litre-atmospheres" as appears at one part of the book. In places the terms ampere and volt are muddled up. Thus on p. 156 we read of a *current* of 72 *volts*, while in giving directions for performing some of the electrolytic experiments the current is defined in terms of "accumulators" without any mention of the resistance of the circuit. As an experiment to show that the direct contact of metals has very little effect in developing electro-motive force, the author says: "Copper wires are soldered to a nickel and a silver wire, and these wires are laid on a galvanometer; when the wires are thoroughly cleaned and then pressed one on the other, the needle remains at rest". Of course the needle remains at rest; in this form of experiment it would do so, however great the contact E. M. F.

The name of the translator is sufficient guarantee that this part of the work has been efficiently done.

*Annotationes Zoologicæ Japonenses*, Auspiciis Societatis Zoologicæ Tokyonensis. Seriatim Editæ. Vol. i., parts i. and ii. Tokyo, 25th May, 1897.

The above-named publication marks a new departure in the advancement of Zoology in the Far East. As explained by Professor Mitsukuri in an admirable historical introduction, written in choice English, it is an extension of the "foreign language part" of the *Zoological Magazine of Japan*, now in its ninth volume—in effect it is an *Anzeiger*, in which articles will be admitted in English, German, French and Italian, primarily by way of relieving the *Journal of the College of Science of the Imperial University* of less formal or preliminary notices and of making the progress of Zoology in Japan known abroad. We heartily congratulate our Eastern friends upon so heroic a course, and recommend this to workers in certain other countries which stand in a somewhat similar relationship to the great European nations, who are at present disposed to retard progress by writing only in their mother tongue. In detailing the events which have led up to the foundation of the *Annotationes*, Professor Mitsukuri emphasises the interesting fact that as early as the eighth century in the Christian era there was already established in Japan a University with four departments; and in tracing the influence of knowledge upon the destinies of his native land, and upon its scientific productiveness which is of quite recent date, he attaches much importance to the efforts of a band of earnest Japanese physicians who in the middle of the eighteenth century mastered the Dutch language, with a view to ascertaining something of western medicine. Proceeding to later events of historical interest, he deals as gracefully as gratefully with the foundation of the modern school of Zoology in Japan, in 1877, by Professor Morse,

and the introduction into it of modern methods of technique by Professor C. O. Whitman. Passing to subsequent years, he naïvely veils reference to his own share in the work in delicate allusions to his *confrères*; and it is for us to add that he will rank as the one man who gave the movement the final impetus which ensured success, and that no name will be more memorably associated with its history than his own. The body of the *Annotations* contains six papers, of which three are wholly systematic, illustrated by three plates which, though somewhat crude, are truthful and expressive (*i.e.*, they are Japanese!) and by woodcuts, and there follow some "Miscellaneous Notes" and a report of the monthly meetings of the Zoological Society of Tokyo. The appearance of the names Mitsukuri, Ijima, Ishikawa, Goto and Kishinouye, among contributors and responsible promoters, is a sufficient guarantee of the value of the work; and the record of new and remarkable species of Chætognatha, of experiments on the accommodation of Infusoria to certain solutions, of the changes with advancing age in the calcareous deposits of *Stichopus*, with a revision of Hexactinellids with discotasters, is a sufficient testimony to its breadth and novelty. The growth of holothurian "spicules" is a subject which has already occupied the attention of Japanese zoologists, and the afore-mentioned paper on the process in *Stichopus*, which is by Professor Mitsukuri, has an especial interest, since it furnishes support with extension to Australian forms to Théel's conclusion that *Holothuria armata* (Sal.) is but a form of *S. japonicus*, and suggests that the *bêche-de-mer* question would appear destined to final solution at the hands of an eastern zoologist.

The publication is a legitimate outcome of noble work performed for its own sake, and we wish it the success and support it deserves.

It is moreover anticipatory, as we gather from Professor Mitsukuri's remarks, to the transfer of the Marine Observatory at Misaki, which is now famous in the annals of Zoology in the Far East, a couple of miles northwards, with considerable enlargement.

For several years past the activity of Japanese biologists has been a subject for comment and admiration by the world, and be it remembered that it has lately yielded us one of the most important among post-Darwinian discoveries in Botany. From recent events the zoologists would appear to be following closely in the wake of their American brethren on the opposite shore of the North Pacific, in a manner amounting to friendly rivalry. Recent work upon the chimæroid fish *Harriotta*, the deep-sea gastropod *Pleurotomaria*, and the remarkable cephalopod *Opisthoteuthis*, justifies this assertion; and in view of it no little interest attaches to an announcement from the United States, which followed close on the publication of the *Annotations*, that there would appear in June of the present year in connection with the *American Journal of Morphology* a *Zoological Bulletin*.

Professor Mitsukuri remarks in his introduction that the *Annotations* will for the present be issued quarterly, and the editors of the *American Bulletin* anticipate that material will be forthcoming "for at



least six numbers a year". The one, as we have intimated, is, and the other it is promised shall be, of the nature of an *Anzeiger*, to contain but preliminary notices and contributions of a brief and desultory nature—*i.e.*, a running record of passing investigation. We beg of the promoters to adhere to their original scheme for both the contents and rate of issue of these most useful publications; and in the name of the teachers in our higher colleges and of responsible heads of establishments devoted to zoological research, who now-a-days are overwhelmed in the sacrificial task of endeavouring to keep pace with current literature, we exhort them to exclude lengthy dissertations, and to curtail to the utmost discursive and polemical ebullitions, since, by the introduction of such things, the scope of certain allied periodicals has become so enlarged that their original objects have been exceeded and their too rapid appearance has become a burden. And we sincerely hope they will not allow their pages to be frittered away in scrappy unillustrated diagnosis of new genera and species, begotten of a weak-minded craving for priority, such as are at times admitted wholesale into those of contemporary periodicals.

*Lehrbuch der Zoologie.* Von R. Hertwig. Vierte umgearbeitete Auflage. Jena: G. Fischer, 1897.

The present edition of this well-known work exceeds its predecessor in length by but thirteen pages. The general arrangement of its contents remains unaltered, and we still meet with the insufficient treatment of the vertebrata and scanty recognition of certain invertebrata so characteristic of the earlier editions. The leading modifications, as explained by the author in his preface, are the reconstruction of the chapter on the Sporozoa and the utilisation of Boulenger's classification of the Reptilia. The former is largely associated with an incorporation of the writings of Wasielewski, whose figures of *Coccidiam* replace those of Hatschek, and from which Labbé's *Hæmamaeba laverani varietas quartana* is adopted. The Gregarinidæ are dealt with as an order of the class Sporozoa; and, conversely, the Ophiuridæ, in previous editions regarded as an order of the class Asteroidea, are now elevated to class rank. The Trilobita, hitherto with the Xiphosura and Gigantostraca disposed of in an *Anhang* to that portion of the work devoted to the Entomostraca, are now dealt with as an order of this sub-class by recognition of the epoch-marking discoveries of Beecher in *Triarthrus*. In effecting the latter radical change in his work by the incorporation of irresistibly important observations in palæontology, the author has laid himself under an obligation to similarly modify other sections of it which deal with groups of animals the inter-relationships of which have been during recent years rendered specially clear by the discoveries of palæontologists. Seeking the fulfilment of this, we note that the incorporation of Beecher's work is accompanied by a fuller recognition of the Rhynchocephalia, but of the allied "Eotetrapoda" of Credner and the wonderful series of anomodont reptiles which Seeley has during the last few years described, many of them being

annectant forms the importance of a knowledge of which is to the elementary student at least as great as that of *Triarthrus*, we find no mention. Nor is the palæontological portion of the book alone thus weak and behind the times. Two and a half years have elapsed since the publication of the previous edition of the work, and during that period it has been discovered that some Marsupials develop an allantoic placenta; and in *Anaspides tasmaniæ* there has been described a living Crustacean combining characters diagnostic of the Amphipods, Schizopods, and Decapods. Half a dozen investigators have during the period radically revolutionised our knowledge of the tooth-genesis of the Marsupialia; but of these and numerous other topics which, like them, are landmarks of contemporary investigation that have necessitated a reconsideration of first principles of classification and of our accepted views of phylogeny and structural relationship, we find no mention in the book. The remarkable treatment of the Bryozoa, Brachiopoda, and Tunicata, upon which we have previously commented, is still persisted in; and we would again point out that *Rhabdopleura* and *Cephalodiscus* are important forms which should be made known to even the elementary student, while annectant types such as *Acinetoides* among Protozoa and the Nothosauria among reptiles might well have been alluded to, when, on the author's own showing, pages dealing with the Protozoa and Reptilia have been materially rearranged. When we consider that the accumulation of zoological literature during the last twenty to thirty years has been of a phenomenal order, unparalleled by that of any other branch of science, and the consequent colossal nature of the task of compiling a text-book of the subject, we feel profoundly grateful to the author of the present work for what he has done. His book, however, good and sound so far as it goes, is thin, and we would have more of it, while more and better illustrations are sorely needed to do even justice to the text. Beyond the new illustrations already alluded to and some trivial modifications in others, there is introduced in the present edition but a drawing of a bird's skull. The replacement of Leuckart's time-honoured figure of *Distomum hæmatobium* by a far better, delineating with some degree of clearness the remarkable relationships of the female to the canalis gynæcophorus of the male, is indicative of promise for the future, for in the reproduction *ad nauseam* of antiquated illustrations our current text-books of zoology are not to be beaten.

*The Life-Histories of the British Marine Food-Fishes.* By W. C. McIntosh, F.R.S., and A. T. Masterman, B.A., B.Sc. London: C. J. Clay & Sons, 1897.

This volume of 467 pages is very welcome, and comes as the realisation of a long-cherished desire of all interested in fisheries work in Great Britain. It is defined by its authors as "a popularised epitome of the results achieved by British and foreign scientific workers at the St. Andrews Marine Laboratory and elsewhere". All our commercially important fishes, with other species to the total number of nearly ninety,



come under consideration, and by way of illustration there are twenty beautifully executed plates, largely coloured, together with a number of maps, woodcuts and tables. The work opens with a short preface, in which its objects and scope are first defined and a contrast is drawn between our present knowledge of the subject in hand and that of 1883, the year of the Great Fisheries Exhibition and of the Royal Commission on Trawling; and there follows an Introduction, in which there are considered the attitude of the public mind towards fishery questions, the present stage of the fishing industry in the evolution of human affairs, together with some historical and preliminary remarks, in which among other things the authors assert (not without justification) that in the past "authorities entrusted with the patronage of posts in which marine zoology could be studied, as a rule and with singular impartiality filled them with those accustomed to other departments of the subject, while men imbued with enthusiasm for marine zoology were stationed far inland". A great deal of emphasis is in various parts of the book laid upon the Trawling Commission afore-mentioned, with allusion amounting almost to reverence for the late 13th Earl of Dalhousie, its chairman, to whose memory the present volume is dedicated. The main contents of the book are sharply divided into two parts; a first and lesser part of 113 pages, which deals with the more general structure of the eggs, and the broader aspects of the life-history, development, and rate of growth of the fishes, and a second and greater part of considerably over 300 pages, in which the life-histories of the species of the several families are more fully considered. It is in the illustration of more especially the latter that the twenty plates have been drawn; and in that of the former there are a series of excellent woodcuts, which delineate the young stages of some of our more familiar food-fishes and were originally drawn in illustration of a famous lecture delivered by the senior author before the Royal Institution in 1889. When, in 1875, Professor McIntosh published his treatise on the *Marine Invertebrates and Fishes of St. Andrews*, expectation ran high, for it became evident that a master mind was intent on the systematic study of the rich fauna of that locality. The Royal Institution lecture was followed by the publication in the *Transactions of the Royal Society of Edinburgh* of an extensive monograph, in conjunction with Mr. E. E. Prince, now Dominion Commissioner in Fisheries, Canada, "On the Development and Life-histories of the Teleostean Food and other Fishes," perhaps the most generally interesting and important contribution to the subject that has yet appeared by British authors. Treatise, lecture, monograph, are now seen to have been stepping-stones in the formation of the book under review, while the numerous magazine articles and official reports which the senior author has in the meantime put forward have long led us to speculate upon what would be possibly forthcoming in it. The determination of the identity of the eggs and young of our familiar food fishes, found as they are among heterogeneous assemblages on the surface and in the shallower waters of the ocean, is a perplexing task, demanding great patience and technical skill, which during only the

last fifteen years has been systematically taken in hand by British workers, and in bringing together the sum of our knowledge concerning these this book marks an epoch in the advancement and popularisation of practical fishery affairs. Its only compeer of English origin is Cunningham's *Marketable Marine Food-Fishes*. It, however, transcends that, and on perusing it we confess to a feeling of pride in the amount that is really known and experimentally established, and of profound gratitude to all connected with St. Andrews for their noble share in the work.

The book has further a special interest since it is the first important publication which has emanated from the Gatty Laboratory of the University of St. Andrews, over which Professor McIntosh presides. The presentation of this building as a mark of appreciation of its director's epoch-marking labours in Marine Zoology is a matter of such recent history that it calls for no comment here, except to say that it marks an event upon which he and his ancient University are to be heartily congratulated. Professor McIntosh will be remembered in history as a pioneer in the application of Zoology to fishery affairs. The work of St. Andrews, with which his name and the volume under review will be ever associated, stands alone; it has been done on slender means, against considerable odds, and even now that in the establishment of the Gatty Laboratory it has received such deserving recognition from a private source, the miserable pittance allotted it under the Fishery Board for Scotland has ceased. Although the bulk of the observations set forth in the present volume have been made at St. Andrews, among leading investigators whose names occur in the text are Brook, Cunningham, Dunn, Fulton, Green, Haddon and Holt, than whom none have during recent years done more by honest labor to advance our knowledge of British Marine Fishes. The work of not a few foreign contemporaries of necessity comes in for recognition—Agassiz, Whitman, Dannevig, Möbius, Petersen, Sars—and the English Zoologist asked to recommend a series of reliable drawings extending to the later stages of development of the Plaice and Flounder is no longer under the humiliating necessity of referring his applicant to them and them alone. The weakest portion of the book is that dealing with organology and embryological detail. For want of better illustration a great deal of this will miss fire with the general public, to whom the usage of terms such as “periblast” and “intermediate cell mass,” without sufficient definition, can convey little idea. Gross errors we have not detected, but among interesting topics of far-reaching importance we could have wished a record of the presence of one or more spiny rays in the anterior dorsal fin of the Hake; while further details concerning the appearance of similar structures, of cephalic spines, and the development of an air-bladder, among young Pleuronectids, and a mention of the existence, symmetry, and habits of *Psettodes* would not have been amiss. Fuller recognition might have been granted the investigations of Möbius concerning the renal origin of the thread of the Stickleback's nest, so interestingly associated with the contemporary researches of Prince; and a fuller account of the spawning act of the male herring



ought certainly to have been given. Where all has been so well done, however, there is little room for criticism. The book is well up to date, as passing reference to the researches of Grassi and Calandruccio on the life-history of the Eels sufficiently testifies; and its pages teem with detail, set forth in pleasant and enthusiastic terms wholly destitute of pedantry. Among those portions of the book deserving special mention as incurring the lasting gratitude of the student and practical worker are pp. 42-56 which deal with analyses of "pelagic life during the various months" of the year, and pp. 462-463 which bear a "synoptic table of the eggs of marine fishes"; and it may be remarked of the authors that they have utilised the practical fisherman to the best advantage, for example, as concerning the matter (p. 15) of the wholesale devouring of herrings' eggs by the haddock. Their whole attitude is that of devoted workers, men among men, anxious to press into the service of their cause all who are likely to aid it; and to this end due prominence is given to the statement of topics for immediate investigation. It is remarked on p. 66 that in the study of the subject in hand "the zoological investigator is stimulated by the fact that all his labours directly bear on the public welfare" and that although "the state has in past years spent princely sums on more or less pure science, . . . at the present moment the public interests demand . . . the exhaustive investigation of all that pertains to the food-fishes of our shores, since the problems connected therewith affect the prosperity of so large a portion of the population". While appeal is thus made to the state, an enthusiastic tone is struck which pervades the whole book. Under the spell of this the intelligent reader feels himself imbued with an ambition to work out some detail, if only in personal regard for authors who have so nobly bestowed time, labour, and money upon their chosen occupation. And when we consider how vast a field lies unexplored and how fascinating is the work to be done, pending the consideration of the state, we could desire nothing more for the authors than that their book should entice unto them the private workers whose aid they so fully deserve.

*Das Ellenbogengelenk und seine Mechanik.* Eine anatomische Studie, von J. W. Hultkrautz. Jena: Gustav Fischer, 1897.

This study of 144 pages, by the Prosector in Anatomy to the Karolina Medico-Chirurgical Institute of Stockholm, like so much in the domain of comparative vertebrate anatomy which during recent years has emanated from that city, bears the imprimatur of Professor W. Leche, since to him and Professor Lindström the author acknowledges his indebtedness for the material upon which it is based. It is divided into four sections, of which the first three deal minutely with the structure, movements, and development of all parts of the human elbow joint, accompanying tables being introduced where necessary, while the fourth is devoted to a comparative morphological study of the joint in representative members of the classes and orders of terrestrial vertebrata. The work is necessarily of a very technical character, and is begotten of a devotion to the cause of science nobly supported by Dr. Gustav Fischer

in its publication on his world-renowned lines. That portion of it which deals with the architecture and mechanics of the bones as involving an analysis of their "cancellous" constituents is, nevertheless, in a measure fascinating.

The work is illustrated by four plates and twenty-one woodcuts, and so far as we have been able to test its accuracy by appeal to actual specimens we have found it reliable. A lengthy classified bibliography of recent literature is appended, containing a list of papers which deal both with the specific and cognate subjects. The author is careful to explain in his introduction that this is incomplete, and that the whole hand-and-text-book literature is omitted; but, that notwithstanding, we should have expected at least a reference to the investigations of Zaaier on the architecture of the human skeleton, to the recent remarkable papers by Cope on "False Elbow Joints" and "The Mechanical Origin of the Hard Parts of the Mammalia" (upon which we could have wished the author's expression of an opinion), and to the allied observations of Scott and others, intimately associated therewith. The results of the author's laborious researches will ere long find their way into the text-books; and now that the study of arthrology is being put upon a sound basis, it is absolutely imperative that the time-worn misrepresentations of the position of the limbs of the Eared Seals, the Walrus, and the Bats, so long reproduced again and again in popular and elementary treatises, should give place to more accurate representations of fact, if only as a necessary preamble to the treatment of the more exact knowledge of which we are now becoming possessed.

*Papers and Notes on the Genesis and Matrix of the Diamond.* By the late Henry Carvill Lewis, M.A., F.G.S. Edited from his unpublished MSS. by Professor T. G. Bonney, D.Sc., LL.D., F.R.S. (pp. 69, with 2 plates and 35 woodcuts). Longmans, Green & Co., 1897.

By the loving care of his widow these valuable papers of the highly gifted Professor Carvill Lewis—whose early death was so great a loss to science—have been rendered accessible to geologists. The circumstance that the proofs have passed through the hands of Professor Rosenbusch of Heidelberg and of Professor T. G. Bonney of University College, and that the latter has taken upon himself the responsibilities of editorship, afford a sufficient guarantee that the accuracy and scientific character of Professor Carvill Lewis's very interesting memoirs have been maintained.

The book includes a memoir entitled "On a Diamond-bearing Peridotite and on the History of the Diamond," read before the British Association at Birmingham in 1886, and one on "The Matrix of the Diamond," delivered before the same association at Manchester in 1877. In these memoirs the author, besides giving much valuable and original information concerning the mode of occurrence of diamonds in South Africa, establishes the existence and characters of a peculiar type of rock to which he assigned the name of "Kimberlite".



As a supplement to these papers on the South African rock, Professor Bonney has included in this little volume a chapter on the "Kimberlites" from Syracuse, N.Y. and Elliot County, Ky., in the United States. His account of these rocks is based on unpublished notes by Professor Carvill Lewis himself, and on later memoirs by Professor G. H. Williams and Mr. Diller.

It is well known that Professor Carvill Lewis contemplated a complete discussion of the relation of diamond-bearing deposits in different parts of the world to olivine and serpentine rocks. But the notes left on this subject were, in the judgment of Professors Bonney and Rosenbusch, too incomplete for publication with advantage at the present day.

*Electro-Chemistry.* By Max Le Blanc. Translated by W. R. Whitney. London: Macmillan & Co., 1896.

To those unacquainted with the chapters in Ostwald's *Lehrbuch* dealing with the same subject this book will prove extremely interesting, and even to those who are familiar with the views which Ostwald has developed so plausibly the book will be very useful.

Le Blanc's own researches, begun under Ostwald's direction, occupy an important position in connection with the subject, and this fact lends additional interest to the work.

The first part of the book—containing chapters on the dissociation theory, the migration of the ions and the conductivity of solutions—deals very clearly with questions already familiar to the English reader. The manner in which migration data are practically obtained is more fully described than is usual.

The second part—containing chapters on electromotive force and polarisation—will, however, attract much more attention.

It is unnecessary to refer to the contents of these chapters in detail; but one or two points are perhaps worth noticing.

The conception of solution pressure is very useful when an attempt is made to realise the nature of the equilibrium between a solution and an electrode; but the relation

$$\pi = k T \log P/p$$

—where  $P$  is a constant depending on the nature of the electrode—can be derived without the aid of this conception. For this reason the method adopted by Le Blanc of first introducing the notion of solution pressure and then deducing the relation above quoted is open to criticism. The sentence which ends at the top of page 154 needs qualification.

While the author makes no attempt to discuss the nature of the equilibrium between an electrode and a solution in the general case, the view which he takes of the equilibrium in some particular cases seems open to objection. For instance, in the case of an electrode of zinc amalgam considered on p. 159, the zinc may determine the magnitude of the potential difference; but no reason is given why the "electrolytic solution pressure" of the mercury should not determine

the concentration of the Hg ions in the solution. The generality of such an objection is not affected by the fact that, in the case considered the concentration of the mercury ions would be excessively small. The remarks on the *Influence of Negative Ions* (e.g., p. 227) seem open to a similar objection.

In the account of the capillary electrometer, the part played by the acid is not made sufficiently clear. "Chemical Cells" are treated as in Ostwald's *Lehrbuch*, and values for the "Heats of Ionisation" of different elements are tabulated. The source of the energy transformed in the cell (apart from any heat which may be absorbed from the environment) is thus made to depend upon the variation of energy when an element changes into the ionic state. No suggestion as to the nature of the variation is made; but a paper by J. J. Thomson on "The Relation between the Atom and the Charge of Electricity Carried by It" is of interest in this connection.

The chapter on polarisation is the outcome of Le Blanc's own researches. These are of great interest and form a most important contribution to our knowledge of electrolysis generally.

In connection with the theory of gas cells, an experimental determination of the temperature coefficient at different pressures (*cf.*, p. 254) would be very useful. The peculiar position occupied, on Le Blanc's view, (1) by hydrogen amongst kation-producing substances and (2) by oxygen amongst anion-producing substances is worthy of notice. The question of the capacity of the "double layer" at the electrode surface is not considered by Le Blanc. In this respect his work is incomplete for the question is one which is intimately connected with the theory of electrolysis. A considerable amount of experimental information concerning this has been published and it would seem that the views developed in Le Blanc's book can be successfully extended to the elucidation of some of the results.

Finally, since many of the discrepancies which become evident when the phenomena are examined in detail are still unaccounted for, the physical basis of the book cannot yet be said to be perfectly secure. It may however be reasonably held that the "most important term" in the explanation of the phenomena has been discovered. The fruitfulness and utility of the "working hypothesis" can scarcely be questioned. The views developed connect and arrange many of the facts of electrolysis in a very remarkable manner and this is of the utmost importance, for "of all electrical phenomena electrolysis appears the most likely to furnish us with a real insight into the true nature of the electric current".

It should be added that the translation has been very well done, the number of misprints and minor inaccuracies being unusually small.





